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THE CATTLE GRUBS OR OX WARBLER, THEIR BIOLOGIES AND SUGGESTIONS FOR CONTROL

By F. C. BISHOPP, *Entomologist*, E. W. LAAKE, *Associate Entomologist*, and H. M. BRUNDRETT, *Assistant Entomologist*, and R. W. WELLS,¹ *Entomologist*, *Investigations of Insects Affecting the Health of Animals, Bureau of Entomology*

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The cattle grubs (*Hypoderma lineatum* De Villers and *H. bovis* De Geer²) are among the most widespread and injurious insects with which our livestock are beset. Nearly every owner of cattle is familiar with these larvæ, which are found under the skin on the backs of cattle in the early spring. Few, however, connect them with the adult insects which are known as heel flies or warble flies. Still fewer people have ever seen a heel fly, and many stockmen say, "I have heard all of my life of the heel fly and have seen the cattle run from it but I have never seen one." This has led many to regard the fly with something akin to superstition or to consider its existence a myth.

Among scientific workers there is also a very meager knowledge of the true life history or importance of these insects. Although a considerable number of veterinarians, zoologists, and entomologists have made observations and published articles, much of this work has been of a fragmentary character and most of the important biological facts have been established during the last decade. It is the writers' desire to set forth briefly the knowledge gleaned to date, and especially to present facts yet unpublished regarding the life his-

¹ Resigned July 24, 1923.

² Order Diptera, family Oestridæ.

tories, habits, injuriousness, and means of repression of these two species, as obtained during this investigation.³

HISTORY

The heel flies or warble flies, or at least the effects of their attacks, have been known to man from time immemorial. The writings of Virgil and Shakespeare contain statements which undoubtedly refer to these pests. Their peculiar and injurious habits have attracted the attention of many naturalists, zoologists, and veterinarians, and the results of the observations and deductions beginning with the articles on this subject published in 1710 and 1713 by the Italian naturalist Vallisnieri (102, 103)⁴ make very interesting reading. Linné (61), in 1739, published information on the related reindeer bot (*Oedemagena tarandi* L.) and expressed his opinion that the eggs were attached to the skin or hairs and were not pushed through the skin as was believed by all previous writers, and as some subsequent writers have believed.

In 1797 Clark (20) published a notable account for that day of the Oestridæ, including observations on the habits of the cattle grubs. His modified and amplified views were published in 1827 (21) and 1843 (22).

In 1863 the Austrian entomologist Brauer (8) published his monograph of the Oestridæ, which added much to the knowledge of the species. He describes the last two stages of the larvæ, and in a subsequent article (9) he indicates a simple method of differentiating the last larval stages of *H. lineatum* and *H. bovis*.

Most writers up to the time of Clark's observations, and in fact many subsequent writers, were of the opinion that the flies place their eggs under the skin of the host. This idea probably originated from the fact that the cattle are driven to a frenzy by the ovipositing flies, the conclusion being that the flies must sting when laying the eggs—this, despite Linnaeus's statement in 1739 regarding the placement of the reindeer bot eggs on the hairs.

Up to the publication in 1888 by Hinrichsen (41) on the finding of Hypoderma larvæ in the spinal canal, only the subdermal or last larval stages were known. Hinrichsen reported the common occurrence of these (now known to be third-stage) larvæ in the spinal canal of cattle in December, January, March, May, and June. He also concluded, apparently without having seen the egg or the fly ovipositing, that the hosts take up the eggs with grass and that the young larvæ reach the spinal cavity from the diges-

³ The present studies have been carried on incidental to other projects for a number of years and during the last seven years have received major consideration. During the prosecution of the work the writers have been materially assisted by many individuals and organizations, to whom thanks are extended. The Bureau of Animal Industry, through its various agents, has aided by sending immature stages. Dairymen, especially in the vicinity of Dallas, Tex., and Herkimer and Middletown, N. Y., have assisted materially by permitting the use of their cattle in the writers' experiments. Many specimens and much information have been obtained from correspondents, including dairymen, cattle raisers, hide dealers, butchers, packers, and others interested in the problem. The management of the leading packing plants in Dallas and Fort Worth, Tex., have been especially courteous in furnishing material for examination and in permitting examination of cattle during slaughter. Of necessity, a number of entomologists have been more or less associated with the writers in the carrying out of the observations and experiments. The following men have contributed materially to the results as herein given: D. C. Farman, O. G. Babcock, Oscar Pool, E. E. Wehr, H. P. Wood, and W. E. Dove.

⁴ Numbers in italics refer to "Literature cited," p. 114.

tive tract, thence migrating up to the subcutaneous tissues of the back. In 1889 one of these early-stage larvæ found in the brain of a horse by Poulson was described by Boas (5) as a first-stage *Hypoderma* larva. From this time on the veterinarians, especially of Denmark and Germany, made important contributions regarding the young stages within the bodies of cattle.

During the decade beginning in 1884, the English entomologist Ormerod made a number of contributions to the literature of this subject culminating in reports published in 1894 (71) and 1900 (72). In these articles much valuable information is presented, especially as regards losses. This writer entertained the old idea that the larvæ penetrate through the skin of the backs of the cattle.

In America, interest in this pest began to be evident during the eighties; and articles were contributed by Riley (82, 83) in 1889. In 1890 Cooper Curtice published a note (24) reporting the finding of larvæ 10 to 15 millimeters long in the walls of the esophagus, in the pleura near the eleventh rib, in the subcutaneous tissues of the back, and in subcutaneous tumors which opened through the external skin. He states that the finding of larvæ in the early stages in these situations suggests that—

It is possible that the eggs or young larvæ are licked by the cattle from the back; that the larvæ made their way into the esophageal walls and from thence, during the proper season, through the back in the neighborhood of the eleventh rib, to the skin.

Curtice gives in 1891 (25) a full account of his work along this line. This hypothesis was based upon the finding of these immature stages in the submucous membranes of the gullet and in other tissues of the body, often months before the larvæ appeared on the back and cut holes through the skin. He also observed that the larvæ and inflammation disappeared from the gullet by the end of January or early in February. Apparently no observations were made on the actual habit of oviposition of the flies. In 1892 Riley (84) published a very good résumé of the knowledge of the life history and habits of *H. lineatum* up to that date. He concluded from an examination of material from various sources that *H. lineatum* was the predominant if not the only species found in the United States. In this article he also incorporated an account, based on observations of G. Schaupp and others, regarding the actual method of oviposition of this species, and the true first stage was described for the first time. He accepts Curtice's theory of the entrance via the mouth, and concludes that an additional link in the chain of circumstantial evidence pointing toward this method of ingress is supplied by the fact that the eggs are laid largely on the legs and that the cattle lick themselves in that region. In 1897 Marlatt (64) presented a concise summary of the information available at that time.

Horne, working largely on the immature stages within the bodies of cattle, published in Norway in 1894 (45) observations showing that the larvæ are truly migratory. He observed them in various situations, including the spinal column from one end to the other, sometimes under the pleura, in the abdominal cavity, and on the surface of the kidney. The following year the veterinarian Ruser (86) published his observations on the occurrence of the larvæ in the spinal canal and reported that he had found traces of larval tracks in the muscles of the back. In 1898 Koorevaar (54), working

in Holland, gave definite proof that the small larvæ found in the spinal column of cattle were really *Hypoderma*. Some of these were introduced under the skin of a goat, and 12 days afterwards swellings appeared, from which later *H. bovis* was reared. In the same article he also described experiments in which 26 larvæ from the spinal canal of cattle were introduced under the skin of a dog. When the animal was examined two weeks later some of the larvæ were found in various parts of the animal, including the gullet and spinal canal. Similar larvæ fed to dogs and introduced into the gullet of a rabbit through a tube were not recovered. From these tests Koorevaar concludes that in bovines the larvæ reach the gullet or spinal canal after extensive wanderings from the place where they bored through the skin, and that they do not reach the gullet by way of the mouth. Further studies on the migration and seasonal occurrence of the larvæ within the host were published the same year by Koorevaar (55).

Following the publication by Curtice and the subsequent one by Riley, practically all scientists accepted Curtice's theory. In 1903 Koch (53) published a very valuable contribution as the result of several years' study of the larvæ of *Hypoderma* within the bodies of cattle. He shows that the young larvæ are widely distributed within the body cavity and in the intermuscular tissues of the back, and that larvæ as small as 2.2 millimeters in length may be found in the submucous tissues of the gullet. He concludes from the data presented that—

It will presumably be apparent that the entrance of *Hypoderma* larvæ to the bodies of the cattle takes place through the alimentary system and not through the skin, and further that the larvæ migrate through the œsophagus and vertebral canal to the skin.

In 1907 Jost (52) reviewed the life history of *H. bovis*. He concluded that the eggs hatch in the gullet and that the larvæ bore through the mucous lining of it. He also makes the erroneous statement that the life cycle requires about nine months. Sørensen (93) in 1908 discussed the literature and concluded that the larvæ enter by mouth.

During the period 1908 to 1922, Carpenter and his associates in Ireland published a series of papers (12 to 19) dealing especially with experiments with the muzzling of calves in an effort to prevent their infestation. The earlier results were conflicting and the authors changed their viewpoint from year to year. In 1914, however, Carpenter, Hewitt, and Reddin (17) published the results of their observations on the penetration through the skin of larvæ of both *H. lineatum* and *H. bovis*. They first noticed soreness and scabs in the regions near where eggs of *Hypoderma* were attached. Beneath these they found holes indicating penetration and from one of these was squeezed, along with serum, a first-stage larva of *H. lineatum* which had evidently penetrated through the skin at the spot. They followed this with tests of newly hatched larvæ of *H. bovis* placed on clipped hair on a calf and found that they quickly passed down the hair and began to burrow into the skin immediately. They conclude:

We believe therefore that no further doubt is possible as to the entrance of young *Hypoderma* larvæ into its host through the skin close to wherever the eggs may have been laid, and the results of the muzzling experiments show that entrance by the mouth is unlikely.

They have also expressed the opinion that it is not improbable that the larvæ may go from the legs to the gullet and thus to the back. Hadwen, working in British Columbia, has also made some valuable contributions to our knowledge of *Hypoderma*. In a paper published in 1912 (32), he presents data on the injuriousness of the cattle grubs in Canada and adds some valuable information on the method of egg laying of *H. bovis*.

The seriousness of injury by cattle grubs in Germany led to the appointment of a commission to study all phases of this subject. Several years were spent in this investigational work and the results were published in parts in the years 1912 to 1919 (67). A large amount of information was obtained on the losses due to the pests, relative numbers of the two species, life histories and habits, and control work.

C. Stub (95-99) carried on observations on cattle grubs in Denmark and published his records in 1912, 1913, 1915, and 1919. He added to the information on the life history and habits of the insect and reported that, in collaboration with Prof. Phil Boas, he found beneath a number of eggs a burrow through the skin which they interpreted as the entrance hole of a newly hatched larva. Stub also found larvæ from 2 to 7 millimeters long in the subdermal connective tissue of calves. In early records, he concluded that the larvæ burrow directly through the skin, but was under the erroneous impression that the eggs are laid on the back. In 1919 (99) he definitely traced the course of young larvæ from the inside of the right tibia to the esophagus.

Hadwen published further observations on the life history and seasonal development of both species in 1915 (33). In this paper he showed that larvæ removed from the gullet and placed under the skin on the leg of calves would work upward rapidly through the connective tissues and ultimately reach the back. In 1916, Hadwen and Bruce (38) attempted to trace the larvæ as they left the gullet and suggested that they pass up the crura of the diaphragm or along the posterior borders of the ribs to the neural canal and out through the posterior foramen to the subcutaneous tissues of the back. In another paper (34), in 1916, Hadwen added further data on the seasonal development of the larvæ and demonstrated the ability of the newly hatched larvæ to penetrate bovine skin. He also described lesions on cattle chargeable to the penetration of *Hypoderma* larvæ. Later a concise account of the cattle grub problem was issued by Hadwen (36).

In 1920 Carpenter and Hewitt (18) described in detail a successful experiment with warble eradication on Clare Island, Ireland; and in 1922 in the sixth report (19) on the problem, Carpenter, Phibbs, and Slattery presented further information on the life and seasonal history of both species of *Hypoderma* and further experimental evidence that larvæ enter the host through the skin only and not by way of the mouth. This report also summarizes tests with various dressings applied to the backs of cattle to kill the grubs, especially tobacco-powder wash. The biologies of *Hypoderma* and other aspects of the grub problem were summarized by Seymour-Jones (91) and Warburton (110) in 1922.

LIFE HISTORY IN BRIEF

There are two distinct species of cattle grubs and these of course present differences in appearance and habits in each of their stages. In a general way, however, the life histories of the two are similar, and the following summary of that of *Hypoderma lineatum* will serve as an illustration. Beginning with the large grubs which are well known to practically everyone who handles livestock, the life may be traced as follows:

As the grubs reach maturity in the subdermal tissues of the back during the late fall, winter, spring, or early summer, the holes through the skin gradually become larger and finally the grubs crawl out and drop to the ground. They seek protection under any loose material at hand and the outside skin shrinks, becoming hard, and within this the flies develop, emerging from 30 to 60 days later. These flies mate soon after emerging and without partaking of food begin to deposit eggs on cattle. The eggs are laid for the most part on the legs, probably the majority of them being below the knee or hock joint. The eggs hatch in from $2\frac{1}{2}$ to 6 days, depending upon the temperature. The young larvæ crawl down the hair to the skin and immediately begin burrowing into it. At the point of entrance serum usually exudes and rather characteristic scabby and tender areas remain for a few days. After penetration little is known of the minute larvæ from the time they pass through the skin until they appear in the body cavity, especially in the submucous layers of the gullet of the host, having increased considerably in size and become more opaque, and evidently having passed through a molt. They spend several months in the host, mainly in the tissues between the mucous membranes and the muscular walls of the gullet, and evidently, as shown by one of the writers (Laake, 57, 58), pass through a molt in that situation or en route to the back. Growth continues during the summer months, and in the fall or winter the grubs have attained a length of from 15 to 17 millimeters and are ready to start on their migration to the back. Here again the exact route followed is not absolutely known; but these larvæ, which are of sufficient size to be found easily, have been met with in various places in the chest and abdomen and on the diaphragm. Not infrequently they are observed in the spinal canal and a little later are to be found in the connective tissues beneath the skin along the back. A hole is cut through the skin almost immediately after the larva reaches that situation and within 2 to 6 days the larva again molts and a wall of tissue begins to form around it in the form of an encystment sac. The next molt takes place about 24 days later, and the insect is now in its final larval stage. The duration of this stage averages about 30 days. It is thus seen that the development requires approximately a year's time, there being one generation during the year. The major part of this time, from 9 to 11 months, is spent within the body of the host.

DISTRIBUTION

The distribution of the two species of *Hypoderma* affecting cattle has received comparatively little attention, certainly not as much as the subject deserves. It appears that the grubs reach their maxi-

imum development in numbers in parts of Germany. They are known to be abundant in Switzerland, Denmark, Holland, and the British Isles, and probably occur throughout Europe. They are abundant throughout the greater part of the United States and southern Canada.

It is very doubtful if either species of *Hypoderma* will ever become an established pest in the Tropics or subtropics. Both have been repeatedly introduced there with cattle, but there are no records of subsequent breeding. It is true, however, that positive information is very meager as to the presence of *Hypoderma* in parts of the world other than those in which it is a pest. A. H. Ritchie informs the writers that in the West Indies he has never seen the warble except in four animals imported from the United States.

No records are known to the writers of the occurrence of *Hypoderma* in South America. The genus is replaced in tropical America by *Dermatobia*, and its similar injury to hides leads some to think *Hypoderma* is present there.

Hypoderma is not indigenous to South Africa and apparently has never become established through introductions. Lounsbury (62) and Hutcheon (47) state that they have no knowledge of the occurrence of either species of *Hypoderma* in native cattle in the Union of South Africa. Lounsbury says in a letter: "Now and then warbles are found under the skin of animals imported within a matter of months, but I have never heard of any being found in animals bred in the country or here for a number of years."

Howard (46) reports the finding of larvæ of *H. lineatum* in Mozambique, East Africa, but does not say if from native or imported cattle.

James Bequaert has informed the writers that in his extensive work in Belgian Congo he has never seen or heard of an authentic case of the occurrence of either species of *Hypoderma* in that country. He also directs attention to the statement of Roubaud (85), who has paid special attention to dipterous parasites of mammals in Belgian Congo and French West Africa, that he has never seen *Hypoderma* on cattle in that region. In northern Africa, *Hypoderma* evidently occurs. E. E. Austen writes that the British Museum contains a male of *H. bovis* from Algeria near Bône, collected May 5, 1896, by A. E. Eaton. Vaney (104) in 1911, states that *H. bovis* occurs in Algeria. Willcocks (112), in 1918, says that *H. bovis* occurs in Egypt, but whether or not it is a common pest is not known.

In Australia, likewise, neither species seems to have gained a foothold. Tryon, in 1906 (100), and again in 1912 (101) reported the apparent stamping out of a local introduction in the Richmond district. Pound (79) describes the appearance of warbles in imported stock and adds, "It is difficult to assign any definite reason why the cattle grub fly has not become established in Queensland. Evidently the conditions of environment are unfavorable." Smit (92) states that *H. bovis* imported into the Dutch East Indies from Holland apparently failed to establish itself, as no records in native cattle have been made.

Regarding the nonoccurrence of *Hypoderma* in Hawaii, Van Dine and Norgaard (108) write: "One and possibly both of the bot flies attacking cattle have been brought to Hawaii with im-

ported cattle. So far neither of them seem to have become established here."

Hypoderma bovis is essentially a northern form. This point has been brought out by a number of writers. Glaser (29) found that in Germany *bovis* predominated over the northern part of the empire while *lineatum* was more in evidence in the southern part. It is also worthy of note that *Hypoderma* larvæ are much more abundant in northern than in southern Germany (56). A writer (1) in Germany has pointed out that, with the interruption of the control work in that country due to the war, the insect had spread to previously uninfested areas. In Denmark, although *lineatum* is present, *bovis* is far more prevalent. Bequaert (in litt.) says:

In Belgium and France *H. bovis* is by far the most common species, and in some regions quite abundant. I do not know of any record of *H. lineatum* in Belgium. In France that species is very rare and of recent introduction; it was not known there at the time Joly (51) wrote his monograph, 1846.

In fact *H. lineatum* was not recorded from France until 1894 (80). Brauer (8, 9) states that *H. bovis* is distributed from Scandinavia to the southern part of Europe and over Asia, Africa, and North America. He writes that this is the only species found in upper and lower Austria, Styria, and Hungary. He records the distribution of *H. lineatum* as South Russia, Norway, the Balkans, the Caucasus, and England. Vaney (104) reports *H. bovis* to be common in the Lyonnaise region in France. He and his associates (59, 60, 105, 107) observed the number of grubby hides to range during the height of the season from about 12 to 21 per cent in different years. Vaney reports the occurrence of *H. bovis* only in the Lyonnaise region. Third-stage specimens, however, which he sent the writers from the gullets of cattle of that region, prove to be *H. lineatum*. In England and Ireland both species are common but sufficient data are not at hand to show their relative numbers. Hadwen (36) states that in Canada the two species have equal distribution, but that their distribution in the northern part of the country has not been determined. He makes no definite statement, however, regarding the relative abundance of the two.

A. Gansser, chairman of the Warble Fly Commission of Basel, Switzerland, states in correspondence that both *H. lineatum* and *H. bovis* are present in that country. *H. bovis* apparently constitutes about 60 per cent of the total number. The insects appear to be very abundant in certain sections of that country. Gansser states that they are generally distributed in the Alps and Jura Mountains up to 6,000 feet. He mentions heavy injury in the cantons of Valais, Vaud, and Grisons. Bornand (7) also comments on the abundance of *H. bovis* in cattle of the Jura and the Alps.

Until recently practically nothing definite has been known of the occurrence of *Hypoderma* in India. Maxwell-Lefroy and Howlett (66) write:

It seems probable that *Hypoderma*, the common European genus, is confined to western India from the Punjab southward probably as far as Gugerat. O'Quinlan (superintendent, C. V. D., Bengal) informs us that he has rarely or never seen warbles in Bengal cattle, and this agrees with our experience.

Patton (75) secured a specimen of *H. lineatum* from Doctor Anandale from India in 1922 and later others were sent him by Capt. H. E. Cross, who at the same time sent to the writers specimens of

several larval stages of *H. lineatum* from the Punjab. He also furnished data showing an infestation of slightly over 35 per cent of some 41,000 head of cattle which he examined in different parts of the Punjab. C. W. Howard has written that he has never seen *Hypoderma* larvæ in southern China, except in cattle that were being imported. C. P. Clausen made some inquiry regarding the occurrence of *Hypoderma* in Manchuria in 1923. He informed the writers that although cattle in that Province were not infested, those from Mongolia were heavily infested. Clausen's informant stated that although many infested cattle were brought into Manchuria from Mongolia, they became free from grubs in one year. Clausen also learned from Dr. H. Okamoto that near Sapporo, Japan, there is a small locality in which this pest has become established, probably through introductions of cattle from America. Doctor Mat-

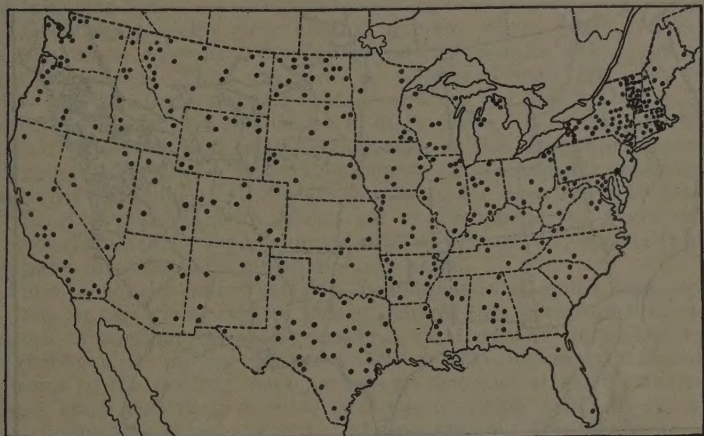


FIG. 1.—Distribution of *Hypoderma lineatum* in the United States. Each dot represents a locality where this species has been collected during this investigation

sumura also informed Clausen that *H. bovis* occurs on cattle in the vicinity of Akita.

Through correspondence and by personal examinations by agents of the bureau, the distribution of the cattle grubs in the United States and their relative abundance have been determined with fair accuracy. A summary of the information on this subject was published by one of the writers in 1915 (4), and Mote (69) has made a valuable contribution regarding the distribution of *Hypoderma* in Ohio. A study of the accompanying maps (figs. 1 and 2) will best illustrate the distribution of the two species of *Hypoderma* in the United States. It is apparent that *H. lineatum* is much more widely and generally distributed in this country than is *H. bovis*; in fact, the entire area where *H. bovis* occurs is also infested with *H. lineatum*. The former species had never been recorded in the United States up to 1910 (50). Riley (84), basing his information on a number of collections mainly from the Central and Southern States, concluded that probably *H. bovis* did not occur in this country. Hadwen (32)

in 1912 showed that *H. bovis* occurred in abundance in southern British Columbia, and further evidence of the distribution is given by Hewitt (42) in 1914. Hence it is problematical as to just when that species was introduced, if in fact it is not a native. Records indicate, however, that it has been introduced rather recently. *H. lineatum*, on the other hand, has been known in this country for many years and has been bred from the native bison, suggesting the possibility that that form may be in reality an American species and not introduced from Europe. As indicated by the map, *H. bovis* is now generally distributed in the Northern States from Illinois to Maine and occurs in more or less isolated areas throughout the Northern States to the Pacific.

As stated by one of the writers (4) in regard to *H. bovis*, this species "must have some well-marked climatic barriers which have

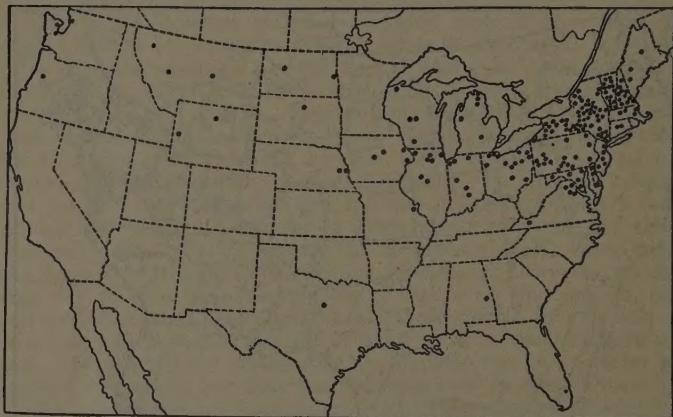


FIG. 2.—Distribution of *Hypoderma bovis* in the United States. Each dot represents a locality where this species has been collected during this investigation. The points shown in the Southern States are collections of larvae shipped in in cattle

prevented its general dissemination through the country." As also pointed out in the publication referred to, there are certain areas in the United States which are almost, if not entirely, free from grubs. The most notable example of this is in the valley of the Red River of the North. In the southern two-thirds of Florida grubs are apparently not to be found except in imported animals. This condition may be due to some combination of natural-control factors, as humidity, salt spray, and drainage. In eastern Massachusetts, the coastal area of New Hampshire, and parts of southwestern Illinois, grubs are relatively scarce. Similar areas of scarcity have been noted by Hadwen in Canada, and he has also observed that the warbles are more abundant in the western Provinces than in the eastern. The writers' observations and reports from stockmen indicate that there is a marked variation in the abundance of grubs in different localities even when not distinctly separated. Sufficient data are not at hand for drawing final conclusions in regard to the

areas of unusual abundance or scarcity; but it is believed that the effect of drainage, soil conditions, and the presence of certain types of vegetation are factors. In general, the lighter soils and good drainage, especially in the areas of heavy rainfall, appear to be favorable to the development of grubs. The presence of timber or moderately heavy vegetation also seems to favor them. There appears also to be an inhibiting influence existent along the coast, especially on the Atlantic.

It has not been possible to determine any special correlation between altitude and the abundance of grubs. It has been noted, however, that they seem to thrive admirably in fairly high altitudes. This is especially true with *H. lineatum*, which is known to be abundant at elevations above 7,000 feet. Some reports received from hide dealers indicate that they think grubs relatively fewer in numbers in the mountain ranges, but the writers' observations do not bear this out.

The evidence seems clear that in general where cattle are kept on the range, especially during the spring months, the grubs are more abundant. This condition is associated with the care the cattle receive, the absence of protection from the flies by barns and sheds, and the lack of cultivation of large areas. It is also probable that the poor and weak condition of stock on the range during early spring gives the flies a better opportunity of successfully depositing their eggs on them. Cultivation is apparently destructive to many of the larvæ, although the reduction in the number of grubs may be brought about by the combination of conditions which usually accompany intensive cultivation of large areas.

There is considerable variation in abundance of grubs from year to year in any given region, but in general this variation does not prevail throughout the entire country. Statistics on the percentage of grubby hides during the years 1921 to 1923, inclusive, furnished by some of the leading meat packers as recorded at their principal plants, show a distinct increase (average of 10 per cent) in grubbi-ness during this 4-year period. At first thought this might be attributed to seasonal conditions; but the fact that this increase was greatest and most consistent in the North, where *H. bovis* is known to be gaining a foothold, indicates that it may really be due in part at least to the spread of that species. If this is true, a very considerable further increase in percentage of grubby hides and degree of infestation may be expected.

ECONOMIC IMPORTANCE

That grubs are highly injurious to cattle is generally conceded. Opinions vary greatly, however, as to the exact extent of the injury, and it is a difficult matter to determine with any degree of accuracy the ill effects caused through the activity of the various stages of these insects. Injury is produced in a number of different ways. These may be classed in two general groups—(1) annoyance caused by the flies during the deposition of eggs, and, (2) irritation produced by the larvæ within the bodies of the hosts. The first group, of course, varies with the abundance of the insects and also with the species present. *Hypoderma bovis* causes the most excitement to stock and hence, where it occurs, produces the greatest dam-

age in this respect. Losses caused by this annoyance include marked reduction in milk flow, failure to put on flesh normally, mechanical injury due to the wild efforts of the animals to escape attacks, and not infrequently loss from the miring down of cattle when they rush into ponds or mud holes, or their injury or destruction when running over embankments or cliffs. These attacks usually occur at a time when the stock are in a weakened condition in early spring, hence the danger of miring and abortion is increased. The exasperation and often-death loss resulting from stampedes caused by heel flies is well known to stockmen. The second group may be divided into four sections: (1) The soreness and pain produced by the penetration of the young larvæ through the skin; (2) the irritation produced in the gullet and in other internal organs due to the migrating larvæ; (3) inflammation produced along the spinal cord and on the main branches of the nervous system by the burrowing of the larvæ along the spinal canal and the ingress and egress of that canal; and (4) the irritation produced by the later larval stages in the subdermal tissues of the back, with accompanying pus formation.

The exact extent of loss produced by these various stages and activities of the insect can not be determined, but it may be well to point out some facts along this line. Considering the loss produced by the flies at the time they are depositing eggs, many dairymen affirm that they know immediately by reduced production of milk when the heel flies become active. Of course the amount of loss at this time depends to a large extent upon the number of flies, the quantity of feed supplied the cattle, and the protection afforded them during the day. In regions where the grubs are abundant some dairymen estimate the milk loss at from 10 to 25 per cent during the period of fly activity. The season when the adult flies are active varies, lasting from one to four months. It can be well understood how this marked reduction in milk flow is brought about when the frantic efforts of the cattle to escape attack are observed. They are frequently seen standing closely bunched in the shade or in the middle of a pond or stream during the major part of the day when they should be grazing.

The annoyance produced by the penetration of the young larvæ through the skin is by no means small, although the period when it occurs is comparatively short. This irritation is indicated by the violent licking of the heels and other parts where the penetration is taking place, accompanied by intermittent kicking and stamping of the feet. There are also extensive external lesions, their location indicated by hair matted and rough from the exuding serum and sometimes by rather extensive areas denuded of hair or even by sloughed areas. This injury is more severe in the case of *H. lineatum* than with *H. bovis*, owing to the fact that with the former many larvæ penetrate the skin at nearly the same spot, the eggs from which they emerged having been laid together, whereas the eggs of the latter are placed singly.

Little is known as to the annoyance produced by the migration of the first-stage larvæ after they have passed through the skin. It is possible, however, that this is of minor importance. As the larvæ increase in size, and especially when they are numerous, there is no doubt that their migration through the body influences the

productivity and health of the host. When the larvæ reach the esophagus in numbers, however, marked irritation is often in evidence. The submucous tissues are edematous, usually yellowish, and sometimes bloody in the region of the larvæ. Cases are on record in which heavy infestations of the esophagus produced edematose conditions with large swellings. Instances are also recorded in which the larvæ burrowing along the spinal canal have caused paralysis of the posterior parts, although this seems to be unusual, considering the large number of cases in which infestation of the canal occurs.

Abundant testimony is at hand as to the injurious effect of the last-stage larvæ under the skin in the backs of cattle. Many stockmen believe, and their opinion in most cases seems well founded, that heavy infestations of the grubs in the backs of calves are a prime factor in causing their death. It has been observed repeatedly that where these larvæ are removed, the calves begin to "pick up" promptly. The effect of heavy infestations in the backs of dairy cattle is also responsible for decreased milk flow. Danish literature contains a reference to a case observed by Boas (6), in which a cow producing daily from 30 to 32 pounds of milk increased the yield to 40 pounds a few days after 80 larvæ had been extracted from the back. Feeders frequently comment on the difficulty of fattening animals in which a considerable number of grubs are present. Those who feed steers on an extensive scale during the winter have informed the writers that in most cases when an animal is not making proper gains, it will be found upon examination to have a heavy infestation of grubs in the back. When these are extracted the animals usually respond well to the feed. Exact information on this subject is meager. Schöttler and Glaser (88) have reported upon an experiment which they performed in Germany on the effect of grubs on the fattening of cattle. The grubs were extracted from one-half of the herd and the other half kept as a check. The portion from which the grubs were removed showed a gain in weight of 5.16 per cent over the infested portion of the herd.

Aside from the damage produced by the holes cut in the skin, there is other injury produced to the host itself by the grubs while located in the subdermal tissues of the back. When the young larvæ first reach the subcutaneous tissues along the back, marked swellings are often produced. These are evidently painful, as indicated by the action of the host when they are touched. Just how much irritation is produced after this is problematical. Undoubtedly the spiny armature of the fourth and fifth stages causes considerable irritation, but it is supposed that the encystment sac surrounding the larger larvæ is practically free from nerves, and for this reason the host probably does not experience any considerable amount of pain or annoyance. Not infrequently, however, pus organisms gain entrance to the openings, and often large abscesses are formed under the skin. These are associated usually with the death of the larva, either by crushing or by its imprisonment and suffocation from the firm plugging up or scabbing over of the hole in the skin. In a number of instances abscesses have been observed which were half as large as the crown of a man's hat and very sore. If these are well opened and drained they soon heal, but where they are not

properly drained they may discharge for considerable periods, and sometimes large encystments occur which may form a permanent blemish on the animal.

Another injury of distinct type, but directly connected with the infestation with grubs, has been discussed by Hadwen and Bruce (39). They have shown that the injection of the juice of a few grubs into a bovine may cause death by anaphylactic shock in a few minutes, and that the crushing of a number of grubs in the back of an animal may cause marked anaphylactic symptoms. Their explanation of this is that when an animal has been infested with larvæ of *Hypoderma* it becomes sensitized, and if the contents of grubs are introduced either by absorption through natural crushing of the larvæ in the back or by injection into the animal, anaphylactic symptoms are produced. In nature cases of anaphylactic shocks are probably rather rare, though they might follow the crushing of a considerable number of larvæ in the back of an animal, as sometimes happens.

In addition to the direct effect of the larvæ on the host itself, there is also an influence on the value of the meat as human food. The presence of the larvæ in the connective tissues of the back produces a very repulsive if not actually injurious condition in that portion of the carcass. This necessitates the trimming off of the affected parts, frequently resulting in the loss of 2 pounds of meat and at best leaving the carcass unattractive and hence less salable. This infiltrated edematous tissue is yellowish and more or less bloody, and appears watery or jelly-like. It is seldom that more than the connective tissue and fat immediately under the skin are affected.

The loss in the value of hides due to the holes cut by the larvæ is one which can be more nearly figured in dollars and cents than any other. Furthermore, this loss is constantly brought to the attention of hide dealers. Some very interesting information has been gleaned from the replies of about 100 packers, butchers, hide dealers, and tanners in all parts of the country through a questionnaire sent out in 1920. It has been computed from these replies that 19 per cent of all hides handled are classed as "grubby" and over 50 per cent of the hides taken off in grub season are so classed. The method of classing grubby hides varies considerably in different sections of the country. Most packer hides are sold on a grub-selection basis. The percentage of grubby hides is determined by the individual inspection of a sample of each lot of hides. Any grub injury which will permit of a skewer being pushed through is considered a grub hole. Country hides are usually sold "flat for grubs;" that is, the percentage of grubby hides is not determined by inspection, but the price is reduced during the grub season sufficiently to cover the lowered value of the hides.

On the Chicago market it is the custom of the trade to inspect, for grubs, branded cow hides and Texas steer hides from November 1 to June 1, Colorado steer hides from December 1 to June 1, and all other classes except bull hides from January 1 to June 1. It is obvious that these periods do not fully cover the seasons of grub damage; for instance, in the Northern States where *H. bovis* occurs, some grubs are present throughout the summer. Bull hides and calf-

skins are seldom classified as regards grubs. On this market it is customary to place all packer hides with five or more grub holes in grade No. 2 and discount them 1 cent per pound. With a country



FIG. 3.—“Grubby” hide after being tanned, practically ruined by holes made by cattle grubs in most valuable part

hide, one grub hole makes a No. 2. Some recognize a No. 3 grade, placing in it all hides with more than 10 grub holes. Extremely grubby hides are frequently called “pepper boxes” (fig. 3) and are sold as glue stock at one-half price. The discount for grub holes in

leather varies considerably, but usually ranges between 3 and 10 cents per pound, according to the number of grub holes in the side.

Practically all those concerned in the hide and leather business agree that the scars resulting from grub attack are not desirable in leather, but the opinion as to the percentage of injury produced differs considerably. Some say that even when completely healed grubby hides are undesirable in their business, on account of appearance, weaker fiber, etc.

It is generally agreed that the nominal discount of 1 cent per pound applied to grubby hides (grade No. 2) by trade custom is far too low. Many tanners state that they would gladly pay double the 1 cent per pound additional charged for hides of No. 1 grade if they could obtain grub-free hides. In fact, tanners of hides for certain purposes make every effort to avoid the grub season in purchasing their stocks; and this practice, in addition to tying up considerable capital for several months, introduces another indirect loss. Under present methods of storing green salt hides there develops in them, when held for several months, a condition known as "salt stain" which materially damages them. This loss is in a large measure chargeable to the warble. There are also a number of tanners who are purchasing Argentine and other foreign hides primarily to avoid grub damage. Grub holes are especially to be avoided when the leather is to be used for certain purposes; for instance, in upholstery leather even one or two holes coming in the center, as they usually do, would cause the entire hide to be discarded for that purpose.

Estimates of the actual monetary loss in hides and leather in the United States due to the grubs run from \$5,000,000 to \$10,000,000 annually. Although the percentage of infested hides varies somewhat from year to year and the number of cattle slaughtered also varies, it is thought that the figures for the winter of 1921-22 are about normal. In the period from November 1 to June 1 of these years, 4,448,793 cattle were slaughtered under the inspection of the Bureau of Animal Industry. It is estimated that about 40 per cent of the cattle killed in the United States that year were under inspection. Thus, the total number of cattle slaughtered in the United States during the period mentioned would be 11,121,980. Accepting the estimate that 50 per cent of these hides are infested with at least 5 grubs each and hence are placed in grade No. 2, we would have 5,560,990 of this grade. At an average of 40 pounds each and applying the nominal 1 cent per pound discount the loss would amount to \$2,224,396. During the same period the number of calves slaughtered under inspection was 2,277,165. By the same method of figuring as for cattle, but considering only 30 per cent of the skins infested and the average weight at 20 pounds, there would be experienced a loss of \$341,575, or a total annual loss among cattle hides and calf skins of \$2,565,971.

Taking into consideration the number of hides which are damaged but not taken off during the season of grub classification, the number which are perforated by less than five grubs, the number which are placed in grade No. 2 or thrown into glue stock at one-half price owing to extreme infestation, the loss through salt stains in storage, and the increased cost of handling in making grub selections of the hides, side leather, and cut leather, and accepting the state-

ment of hide dealers and tanners that the discount of 1 cent per pound is really too small, we may reasonably place the total loss to the hide, tanning, and leather industries of the United States at \$5,000,000 each year. Coppens (23), in connection with a discussion of losses produced by this insect in Europe, states that the War Ministry at Brussels found that the wearing properties of grubby hides as leather is only 30 per cent of that of sound hides. Mason (65) also touches on the importance of grubs to the tanning industry. De Vries (27) and Ostertag (74) also discuss losses in Europe due to these insects.

After a careful consideration of the various losses brought about by the cattle grubs the writers have concluded that they are conservative in placing the annual loss in the United States chargeable to them at \$50,000,000.

INJURY TO MAN

Many cases are on record in which larvæ of *Hypoderma* have been extracted from man. They are found usually in the subdermal tissues, where they produce what is often called "creeping myiasis." There seems to be a tendency for the larvæ to work upward and most of them are finally extracted from the head, face, or upper extremities. These migrations are often extensive and rather rapid, accompanied by considerable pain. In some cases the larvæ appear under the mucous membranes of the mouth.

The source of these infestations in man is not known, but most of them have been in children and usually the affected individuals have been more or less associated with the cattle. It is probable that the flies occasionally oviposit on the hair of the heads or legs of children or on their clothing and the larvæ penetrate the skin upon hatching. In the experience of Glaser (29, *No. 5, p. 35*) while experimenting with the grub, there is an example of the deposition of an egg on woolen clothing. In this case the resulting larva hatched and penetrated the skin of the leg. Some time later its presence in the gastric and esophageal regions was detected by an uncomfortable feeling. The larva apparently passed up the esophagus and was later extricated at the base of one of the lower molar teeth.

Hamilton⁵ records a case of a boy who was suffering for some months from swollen glands on the neck, accompanied by a fetid ulceration around the back teeth on the lower jaw. After three months of unsuccessful treatment a well developed tawny warble larva was discovered in the ulcer at the root of the tongue. The case resulted fatally.

The writers have obtained through W. A. Riley, of the University of Minnesota, the clinical history, as prepared by O. A. Kimble, of a case of dermal myiasis. As this case is typical, and as opportunity has been afforded of examining the larva, a résumé of the case is given. A child 6 years old, living on a farm, was brought to Doctor Kimble's office during the first week in November, 1920. She complained of a swelling of the left forearm with

⁵ Hamilton, John. Medico-entomology. In Ent. News, vol. 4, pp. 217-219, 1893.

some stiffness and pain in the wrist. The pulse and temperature and general physical condition were normal. Three weeks later the child exhibited a swelling of a similar nature in the lumbar region on the left side. This lasted only a few days. During the first week in December the child was again brought in with a slightly edematous area, about the size of the palm of the hand, on the left side in the midaxillary region. Two or three days later this area showed two small perforations of the skin about an inch apart. A similar area next occurred on the lower border of the right scapula. Pain was felt in the area and a few hours later two punctures appeared. A few days later the child's father saw a larva moving in a hole which appeared on the upper angle of the left scapula following a similar clinical experience. Two days later a larva was pressed from a puncture which appeared at the base of the mastoid process of the left temporal bone. This larva was found by the writers to be *H. lineatum* in the third stage.

Another interesting case has been brought to the writers' attention by R. A. Cooley. Dr. O. E. Patterson, who attended this case, and the mother of the infested child have kindly furnished a very complete history of the case. This infestation occurred in a child of 5 years who lived on a stock farm near Moiese, Mont. From late November, 1921, to March 1, 1923, 14 larvæ were removed from the patient. Seven of these appeared on the head and face, one each from the neck, arm, shoulder, and chest, and one each from the thigh and from the calf of the leg. The symptoms accompanying the appearance of each larva were very similar but most acute with those on the face. Several hours (sometimes 24) preceding the appearance of each larva there was malaise and pain in the stomach, accompanied later with marked fever. These symptoms then gave way to retarded heart action, cold limbs, and drowsiness. When these symptoms had practically disappeared a local pain and swelling occurred in the region where the larva came to the surface. The duration of each attack ranged from one and one-half to four days. After several larvæ had been expelled symptoms of neuritis began to manifest themselves in stiffness of the legs, weakness of the leg muscles, and finally almost complete paralysis of the lower extremities, which lasted several weeks, only subsiding after practically all larvæ had come to the subdermal region. A year later this paralytic condition had not completely disappeared. These symptoms suggest that some of the larvæ may have entered the spinal canal and produced lesions there.

The writers have examined two of the specimens from this case and found them to be third-stage larvæ of *H. lineatum*.

Riley (84) has given a rather complete account of the infestation of a child in Pennsylvania. A physician was called to attend this child, which was supposed to be suffering from erysipelas. The child, a boy of 3 or 4 years, was suffering sufficient pain from something working under the skin to prevent his sleeping at night. This larva had been noticed five months before under the skin near the sternal end of the right clavicle, and during the intervening time it had traveled up and down the chest, in front down one arm to the elbow, and over one side to the back. Prior to the calling of the physician no serious annoyance had been experienced. This larva

after removal was positively identified by Riley as *H. lineatum* in the next to the last stage.

Schöyen (89) has presented a résumé of a large number of cases which have been encountered in Norway and elsewhere. He states that he has examined many of these grubs and that they are without doubt *H. bovis*. He further says:

As a rule they have accomplished long ramblings under the skin, always in an upward direction previous to their appearance through an open tumor on the upper part of the body, head, neck, shoulders, etc. All of them have lived in this manner for months and came out in the course of the winter months, but were always still too young to go through their transformation. It is especially with persons who look after or take care of cattle in the summer months that such grubs are to be found during the winter.

It is of course conceivable that these larvæ in their migrations may cause some rather serious symptoms, which in many cases may not be attributed to the larvæ at all.

COMMON NAMES AND POPULAR IDEAS

It is not surprising, considering the wide distribution and common occurrence of *Hypoderma* on cattle, that the insects should have come to the attention of nearly all of the cattle raisers of the country. As with most other insect pests, various colloquial names have been applied to them. In the Southern States the larvæ are commonly spoken of as "wolves" and sometimes as "grubs." In the North and West the term "warbles" is commonly used for the larvæ although they are frequently spoken of as "grubs." By butchers, hide dealers, and tanners throughout the country, the name "grub" is applied very generally to the larvæ of both species and the infested hides are spoken of as "grubby." Certain individuals sometimes also speak of the larvæ as "worms" and others call them "cattle bots" or simply "bots." The term "heel fly" is commonly applied to the adult insect throughout the United States, but in most cases the stockmen do not connect the heel fly with the grub in the backs of the cattle. The term "heel fly" is very appropriate, especially for *Hypoderma lineatum*, as it fittingly describes the habit of the fly in attacking the lower extremities, particularly the heels, during oviposition. "Warble fly" is applied to the adult insect by some stockmen, especially those from England, and "gad fly" is used for it in some localities. The use of the last name is not desirable, as it is more frequently applied to the horse flies (Tabanidae).

In Great Britain the term "ox warble" is used for both species. In Germany the words "Dasselfliege" and "Dasselbeule" are applied specifically to the fly and the larvæ in the back of the host, while "Dasselploge" refers to infestations. In France the word "varron" is used.

There is need for common names to designate the two species. The propriety of adopting the name "ox warble" for the two forms might be open to question, on the ground that the use of the word "ox" as applied to cattle is almost obsolete in this country and that the word "warble" is more aptly applied to the swelling produced by the larva *in situ* and is essentially an English term.

Owing to the aptness and general use of the term "cattle grub," the adoption of this name for the larval stages of the two species is advised. Since *H. bovis* is not to be found in the South but thrives

in the North, the term "northern cattle grub" is suggested for this species; and since *H. lineatum* is abundant and widely distributed throughout the country it may be termed the "common cattle grub." When referring to the adult the word "fly" could be added after either of the names and thus the habits of the larvæ would be suggested; but the well-established term "heel fly," with the modifying words "northern" or "common" preceding it when it is desired to refer definitely to one species, is preferable.

The most prevalent idea as to the cause of the grubs in the backs of cattle is that the animals are stung by the large black horse fly (*Tabanus atratus* Fab.) (fig. 4).



FIG. 4.—The black horse-fly (*Tabanus atratus*), often erroneously thought to be the cause of cattle grubs. Much enlarged

This idea originates from the observation that these flies attack the cattle primarily along the back where the grubs occur and that they annoy the stock considerably. A good many stockmen are of the opinion that the running of cattle in the spring is caused by the pain produced by the grubs in the back, especially at the time they are dropping out. This erroneous supposition is, of course, correlated with the fact that the heel flies are seldom seen in action, owing to the rapidity with which the cattle leave a spot when the heel fly appears. There are many different notions held by stock raisers as to how grubs get into the backs of cattle and what causes them. These

are often colored by the theories propounded by naturalists as reviewed in the preceding historical sketch.

HOSTS

The normal host of *Hypoderma bovis* and *H. lineatum* is cattle, *Bos taurus*. The American bison, *Bos bison*, is known to be infested at times with *H. lineatum*, but bison do not appear to be so heavily infested as are cattle raised under similar conditions in the same regions. The migration and development in bison appear to be practically the same as in cattle.

A number of reports are at hand of the occurrence of *H. lineatum* larvæ in the subdermal tissues of the backs of horses. A few specimens of larvæ from this host have been examined by the writers and found to be *H. lineatum*. Most of those seen were in the fifth stage. Stockmen have informed the writers that occasionally one of their cow ponies becomes infested with as many as 10 or 15 grubs. These sometimes produce abscesses, probably due to the crushing of the

larvæ by the saddle. The writers have no authentic records of the complete development of larvæ within a horse, but this probably occurs occasionally.

Brauer (8) has described a *Hypoderma* larva from the horse and was uncertain of its identity. Ormerod (71) gives considerable information on the occurrence of *Hypoderma* larvæ in horses in England, but none were positively identified. It is very probable that *H. bovis* or *H. lineatum* was concerned in these cases.

The writers have made but a single test of the development of *Hypoderma* larvæ in a horse. On March 15, 1922, and the following day two flies (*H. lineatum*) caught in nature were permitted to oviposit on the hairs, on the feet, and at the base of the tail of a horse. Five days later most of the eggs had hatched and the larvæ had penetrated the skin as indicated by a copious exudation of serum, some of which was slightly tinged with blood. There was also some swelling in the region where the larvæ penetrated at the base of the tail. However, the animal did not show any indication of irritation at the time the penetration took place. In about a week the heavy scab formed by the dry serum loosened. Frequent examination of the host during the next year failed to reveal the presence of a single larva.

Since it appears that *Hypoderma* larvæ may occasionally develop in the goat (*Capra* sp.), several tests were made of this possibility with Angora goats. In 1921, 25 eggs were placed by a fly upon a goat's heels. Three days later some of these were observed to be hatched and the larvæ penetrating, but the animal showed no special uneasiness. During the following spring about 86 eggs of *H. lineatum* were placed on the legs of another goat. Some of these were ready to hatch when the hairs bearing them were cemented on the animal. Other eggs of this lot were shown to be viable by incubator tests, but no lesions could be found on the host. Unfortunately one of these goats was lost the following summer, but the other failed to develop any larvæ. On April 10, 1923, a fly was induced to deposit 61 eggs on the legs of a kid. Although the eggs from this fly were fertile, the host showed no uneasiness and exhibited no lesions of penetration. Apparently the eggs were lost before hatching. No special difficulty was experienced in getting the flies to lay eggs on this host.

On December 22, 1920, 30 larvæ, 10 to 15 millimeters in length, taken from the gullets of cattle, were inserted under the skin between the knee and the hip of an Angora goat. A few days later a careful examination of the skin showed the presence of small objects a few inches from the point of insertion, which were thought to be some of the larvæ. On January 17, 1921, two of the larvæ reached the back in the lumbar region and perforated the skin. These soon scabbed over, however, and on March 4 the lumps were considerably reduced in size, and the larvæ were found to be dead.

Two Angora goats were infested on November 29, 1922, by means of an incision on the lower part of the thigh. One of these received 18 and the other 20 larvæ of *H. lineatum*, averaging 13.2 millimeters in length, from the gullets of cattle. On the former of these two goats 3 larvæ appeared under the skin of the back in the lumbar region, 2 on December 12, and 1 on December 19; and on the latter

2 larvæ appeared on the back December 12, also in the lumbar region. Each larva had cut a hole through the skin, and from these holes there was an extensive discharge of serum which hardened, matting the hair over the grub, thus indicating a marked reaction on the part of the host against the larvæ. All evidence of the presence of the larvæ disappeared in a few days.

During 1922 H. E. Cross forwarded a series of Hypoderma larvæ from goats on the Punjab, India. Most of these proved to be *H. crossi* Patton, but there were two larvæ of *H. lineatum*, one in the fourth and one in the fifth stage.

Peter (76) placed 45 larvæ, removed from the spinal canals of cattle, under the skin of two goats; a single larva finally completed its development.

Koorevaar (54) showed that it is possible for larvæ of *H. bovis* to complete development in a goat after their removal from the spinal canal of cattle and introduction under the skin of the goat.

Brauer (8) records sheep (*Ovis aries*) as a host for Hypoderma larvæ, stating that Winnertz had seen a number of flies following a flock and that Schwabs asserted that grubs occur under the skin of shorn sheep. These he pronounced to be *H. bovis*. It is noteworthy that Brauer placed a question after *Ovis aries* as a host. The writers have never observed a larva of Hypoderma on a sheep in nature, nor have they seen any indication of the attack of sheep by heel flies.

The writers have carried out a few experiments to illustrate how larvæ will develop in sheep. The flies seem averse to laying eggs on the wool, but oviposit readily on the hairs of the legs. Forty eggs attached by a fly above the hoof of a sheep apparently did not hatch, or at least no lesions indicating penetration were observed. These eggs were known to be viable. During the spring of 1922 about 75 eggs were deposited on the legs of a sheep; subsequent examinations failed to indicate that hatching or penetration had taken place. Some of the eggs of this lot were known to be fertile. During the spring of 1923 at least a few eggs of a number deposited on the leg of a sheep hatched and the larvæ penetrated, as indicated by the presence of lesions.

Two grade Shropshire sheep were infested November 29, 1922, by inserting under the skin a few inches above the right hock 20 *H. lineatum* larvæ averaging 13.2 millimeters in length, taken from cattle gullets. These were probably all second-stage larvæ when introduced. On December 7 one larva appeared on the back of one of the sheep, and on December 9 one came up on the other host. Larvæ continued to reach the subdermal tissues of the backs of both sheep at intervals of a few days until January 3, 1923, when a total of 11 had reached the back of each animal. They were rather generally distributed over the backs, but more numerous in the lumbar region. There was more or less exudate from the grub holes, and in no case did the larvæ remain longer than about 10 days before succumbing. Several dead larvæ, all in the fourth stage, were found at different times in the wool.

Many people are of the opinion that Hypoderma larvæ are to be found in small domestic and wild mammals. There are no published records of such occurrence in nature, and the examination of many small mammals in the course of the work leads to the belief that

Hypoderma seldom, if ever, develops in them. Cats are not infrequently infested with oestrid larvæ, but so far as known these all belong to another genus, Cuterebra.

Many dogs kept under conditions which would favor an infestation by Hypoderma larvæ have been examined with negative results. In one instance three adults of *H. lineatum* were permitted to oviposit upon the legs of a dog. About 50 eggs were placed in this way; although the eggs were viable, no penetration appeared to take place. Unfortunately, the dog was lost before an opportunity was had for the larvæ to reach the back.

Koorevaar (54) found that larvæ from the spinal canal of a calf, introduced under the skin of a dog, had migrated extensively when the animal was dissected two weeks later. Some were found in the gullet and some in the spinal canal.

Four tests of the possibility of the development of *H. lineatum* in rabbits were made by allowing the flies to oviposit upon the hairs of different parts of the rabbit. Three of these 4 hosts developed lumps on the body within 45 to 100 days after being infested. Some of these had openings through the skin, but the presence of the larvæ in them was not definitely determined, and none persisted for more than a week or two. In one instance several newly hatched larvæ of *H. lineatum* were introduced into the eye of a rabbit. They were watched for over an hour, but none burrowed into the tissues.

Two experiments were made with the introduction of larvæ of *H. lineatum* from the gullets of cattle into rabbits. On December 22, 1920, 15 larvæ measuring from 11 to 15 millimeters in length were introduced into an incision near the left hip joint of a Belgian hare. The rabbit died from infection two days later. Upon dissection four dead larvæ were found, but none of these were far from the point of introduction.

On November 15, 1922, 10 larvæ of *H. lineatum* from the gullets of cattle were introduced under the skin of a rabbit on the left side of the back in the lumbar region. The average length of these was 14 millimeters. The following morning the rabbit was ill, and had considerable swelling below the point of incision. The infiltrated area extended down the side and under the belly where there was a considerable accumulation of serous material, which was drained. On the second morning the animal was worse, with fever, labored breathing, stiff hind quarters, and an accumulation of puslike material in the eyes. In the afternoon the animal, which was very low, was chloroformed and dissected. Four living and one dead larva were recovered. Two of these were in the connective tissue from $1\frac{1}{2}$ to 2 inches from the point of introduction. One was on the surface of the large intestine about opposite the kidney, and the fourth was rather deeply imbedded in the connective tissue on the inside of the left leg at the knee joint. It was possible to trace this larva with considerable certainty by an infiltrated path down the side to the median line of the belly, thence backward between the legs and upward to the pin bone, and thence to the inside of the leg, the point at which it was found. Thus this specimen had traveled 6 or 7 inches in the subdermal tissue.

In an experiment carried out by Peter (76), several larvæ were placed under the skin of two rabbits. In one of these four living

larvæ were found four months later, but they were not seen subsequently.

A few tests have been made to determine if *H. lineatum* larvæ will develop in guinea pigs. Flies were induced to deposit nearly 100 eggs on 2 guinea pigs on April 10 and 11, 1923. Eggs from these females were shown to be fertile by tests in an incubator, but both guinea pigs apparently lost all the eggs before hatching began.

Several larvæ of *H. lineatum* from cattle gullets were introduced through an incision of the skin on the backs of two guinea pigs. Both animals were somewhat stiff and inactive the following day and the female soon became very sick. An edematous swelling developed on the belly. This finally broke and the animal slowly recovered, but there was no evidence of the presence of the larvæ. The male guinea pig recovered rapidly and a few weeks later developed a small lump with a hole through the skin over it, just behind the shoulders. This was a typical grub lesion, but the larvæ could not be seen. This disappeared in a few days and no further evidence of the infestation was seen.

As is shown in the discussion of "injury to man," infestations of humans, especially children, by *Hypoderma* are not uncommon, although it appears that man is not a favorable host.

ACTIONS OF CATTLE WHEN ATTACKED BY ADULT HYPODERMA

The reactions of cattle to the attack of these insects is so remarkable and so much discussed that a brief statement on this subject seems warranted.

As with the reactions of a host to various other stimuli, we find a marked variation in the effect of *Hypoderma* attack on different individuals. This is, however, mainly a matter of degree of violence of reaction rather than of kind. As has been mentioned, the fright produced by *H. bovis* is much more pronounced than that produced by *H. lineatum*, but the latter often causes a wild stampede.

In the case of both of these species the female has a very flexible telescopic ovipositor, in no way fitted for pricking the skin. In fact it can scarcely be felt on one's hand when it is extended by the fly. Convincing evidence of this is also afforded in the fact that flies have frequently been seen to approach an animal unnoticed and deposit many eggs without any annoyance whatever.

Careful observations among cattle during heel-fly activity will soon convince anyone that it is the attack of the fly which produces the fright. The writers agree with Hadwen (36) that this fear is produced mainly by the persistent attack of the fly. This is particularly true in the case of *H. bovis*. When the fly first attacks cattle at the beginning of the season the reaction against it is usually not very violent. The animal kicks or shakes the foot, but the immediate return of the enemy alarms the cow and she starts walking away; being pursued, the fright becomes more pronounced and she may run a short distance and begin walking again. The fly immediately resumes its attack and then the animal dashes away in terror (fig. 5, b), with the insect often at its heels, in the fashion of a dog. There is reason to believe that the fear of this insect is to some extent instinctive; also that, as the areas of attack become

sore and tender from the penetration of the larvæ, the animals are more easily aroused and terrorized.

After a herd has been attacked for a few days in spring, it is only necessary to have a single fly begin to oviposit on an animal in order to start the whole herd from pasture to some protected place. When water is at hand it furnishes the preferred and most effective pro-



FIG. 5.—Actions of cattle when attacked by adult *Hypoderma*: a, Cow showing attitude assumed when heel fly (*Hypoderma lineatum*) first attacks; b, heifer attacked by *Hypoderma bovis* making wild dash for protection; c, cows standing in stream to escape heel-fly attack; d, calves crowding into shade to escape heel-

tection. Animals have been observed to remain standing in the water practically all day when adults of *H. lineatum* were numerous, and apparently without ever being molested by flies (fig. 5, c), even though the water was not more than a few inches deep. Shade offers considerable protection and is usually sought in the absence of water. (Fig. 5, d.) *H. bovis* is less easily repelled either by water or shade

than is *H. lineatum*. Frequently cattle will run for a knoll if shade is not at hand, and when the breeze is strong the grouping of the stock on high ground seems to give some immunity from attack. When these natural protections are not accessible the flies, especially *H. bovis*, will keep up their attack intermittently, causing the cattle to run from one part of the pasture to another, in small pastures causing them to run round and round until they froth at the mouth, breathe heavily, and even drop from exhaustion. Under range conditions the stock usually have better opportunity of escaping, but the tendency to a general stampede is increased, especially if cattle are being worked in large herds.

When grazing, cattle usually detect the presence of a fly very quickly, largely by sight and hearing, but also by touch. Cattle readily differentiate between the presence of a heel fly and other insects. The listening attitude assumed when a fly is in the vicinity is characteristic, as is also the action of shaking the foot (fig. 5, *a*) to dislodge a fly, the rolling action of the tail, and the look of fright when a fly attacks in earnest.

DESCRIPTION OF STAGES

THE EGG

The egg of *Hypoderma lineatum* (fig. 6, *a*; fig. 7) is dull yellowish white and the surface is smooth and shining. It is narrowly ovoid, slightly larger at the base than at the tip, and its greatest diameter is at the middle. The average length of the egg proper is 0.76 millimeter and the average diameter at its greatest thickness is 0.21 millimeter. The unattached end of the egg has a slight ridge across it from side to side along which the egg splits when hatching takes place. (Fig. 6, *b*.) This ridge crosses the end slightly on the side toward the hair and the micropyle is located centrally at the apex. The clasp with which the egg is attached to the hair is oval in outline. The average length of the base attached to the hair is 0.31 millimeter. The petiole averages 0.1 millimeter in length. It is flat and curved and very narrow when viewed from the side. The position of the eggs when attached in a row is at an angle of about 45° to the axis of the hair, except the last one toward the tip of the hair, which is usually more nearly parallel with it.

The eggs of *H. bovis* are similar to those of *H. lineatum* except in size, measuring 0.81 millimeter in length and 0.29 millimeter in width. The clasping base is slightly more truncate at the end toward the tip of the hair and the petiole arises from the clasp more nearly at its middle than in *H. lineatum*. The most striking difference between the eggs of these two species is the attachment of the petiole to the base of the egg. With *H. lineatum* the attachment is on the side of the base of the egg away from the hair whereas with *H. bovis* the attachment is more nearly in the middle of the base and the petiole is more elbowed. (Fig. 8.) Furthermore, the eggs of *H. lineatum* are normally attached to the hair in rows, whereas with *H. bovis* the eggs are always laid singly.

THE LARVA

FIRST STAGE

The larva of *Hypoderma lineatum* when hatched from the egg measures from 0.55 to 0.65 millimeter in length and from 0.15 to 0.18 millimeter in width at its greatest diameter. The width is greatest at the posterior end and the larva tapers to the head. It is creamy or dull white in color, and densely covered with spines on all segments, the anterior borders bearing the heaviest spines in transverse rows, followed usually by six rows of spines, more or less regularly placed, and slightly decreasing in size toward the posterior border of the segment. The anal segment differs from all those preceding in that it bears spines of three distinct types. The posterior spiracles, which are represented by two dark circular spots, are protected by two or three rather large, triangular spines located near their borders. The cephalo-

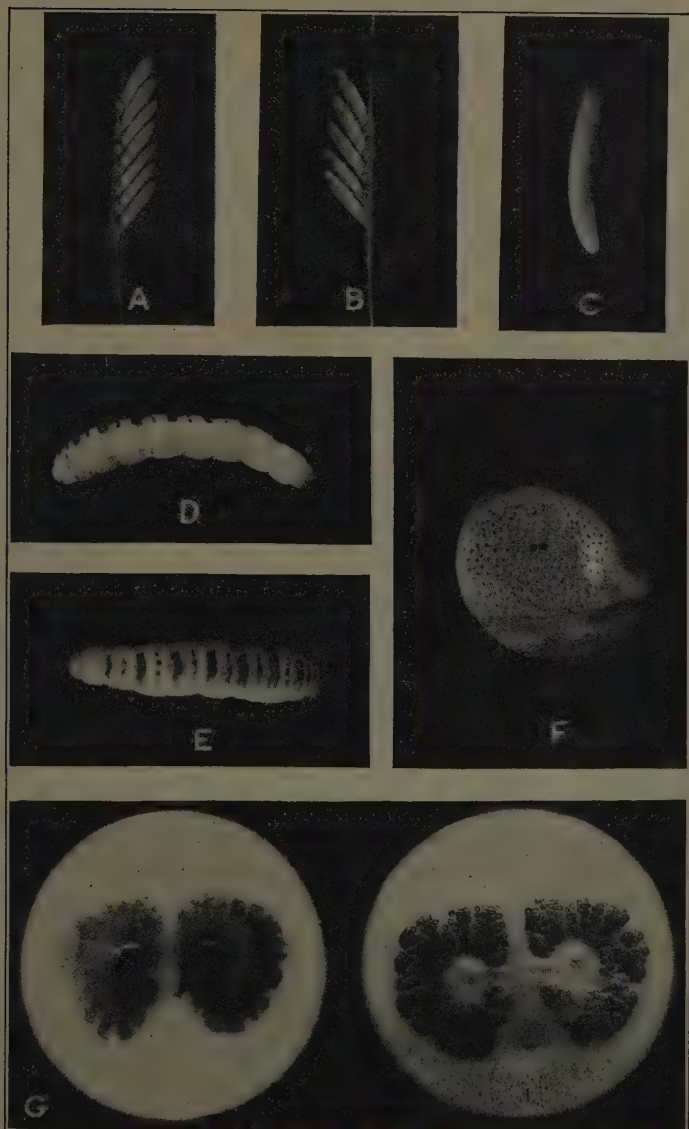


FIG. 6.—*Hypoderma lineatum*: a, Unhatched eggs attached to hair; b, hatched eggs on hair; c, third-stage larva, side view; d, fourth-stage larva, side view; e, fourth-stage larva, ventral view; f, posterior end of third-stage larva; g, posterior end of fourth-stage larva, just before molting (note fourth-stage spiracles in center with fifth-stage spiracles showing beneath); h, posterior spiracles of fifth-stage larva. All much enlarged

pharyngeal skeleton is composed of two long and nearly parallel rods slightly curved outward at the tip on which two crescent-shaped mouth hooks articulate. The hooks are pointed at each end, especially the forward one, which terminates in a sharp point. A prominent inward-curving tooth is located about one-third the length of the entire hook from the anterior tip (figs. 9 and 10). A stout, sharp spine directed forward projects slightly between the mouth hooks. The anterior spiracles appear as two minute circular elevations above the mouth parts and at the tip of the head.

The armature and spiracles of the first-stage larva of *H. bovis* do not differ materially from those of *H. lineatum*, but the larvæ are slightly larger. The outstanding difference is that the mouth hooks of *H. bovis* are well forked at the anterior end and more truncate at the posterior end. The articulation of the mouth hooks is on a small knob extending laterally nearly at right angles to the axis of the pharyngeal skeleton, which is not curved at the anterior tip like that of *H. lineatum*.



FIG. 7.—*Hypoderma lineatum*: Row of eggs attached to hair. Greatly enlarged

SECOND STAGE

The second or next known larval stage of *H. lineatum* found in the esophagus of cattle (fig. 11) varies in length from less than 3 millimeters up to 13 millimeters or sometimes even longer. It is cylindrical in form and tapers slightly at both extremities. The spinous armature is present on all segments. On the body segments the spines are arranged in transverse rows beginning with the heaviest spines along the anterior border and extending well back toward the posterior border. The spines are more numerous per row, thinner, and longer than those of the corresponding segments of the first stage.

The posterior half of the anal segment is covered with stout, sharp-pointed, curved spines; unlike the spines in this group on first-stage larvæ these are provided with a heavily chitinized, large, circular, elevated base.

The second-stage larva of *H. bovis*, which was first described by Phibbs (78), is remarkably similar to that of *H. lineatum* in the same stage excepting the cephalopharyngeal skeleton and mouth hooks, which exhibit the same differences as in the first stage.

THIRD STAGE

The third-stage larva of *H. lineatum* (fig. 6, c), sometimes found in the gullet just before migration to the back, and later immediately after puncturing the skin of the host, is from 12 to 16 millimeters long and from 2.5 to 3.5 millimeters wide. It is cylindrical, with the ends tapering and often with the anal end slightly curved toward the dorsal side. With few exceptions segments 2 to 10 inclusive are free from spines, and at the anterior end only the group of spines below the mouth parts is present. The posterior half of the anal segment is thickly dotted with spines having heavy circular bases greater in diameter than the length of the spine and nearly three times as great as that of the second stage (fig. 6, f). The posterior spiracles measure 14 microns in diameter, and the triangular spines on the border of the spiracles are greatly reduced in size. The form of the mouth hooks, although heavier than in the preceding stages, remains the same.

The third-stage larva of *H. bovis* is slightly larger than that of *H. lineatum*, but the spinous armature shows no material differences. The cephalopharyngeal skeleton and mouth hooks show the same specific characteristics as in the earlier stages (figs. 12 and 13).



FIG. 8.—*Hypoderma bovis*: Egg attached to hair. Greatly enlarged

FOURTH STAGE

The fourth-stage larva of *Hypoderma lineatum* (fig. 6, d, e, g) is from 13 to 18 millimeters long and from 3.5 to 6 millimeters wide. It tapers considerably from the fourth, fifth, or sixth segments to the posterior extremity. The spinous armature varies greatly with different specimens.

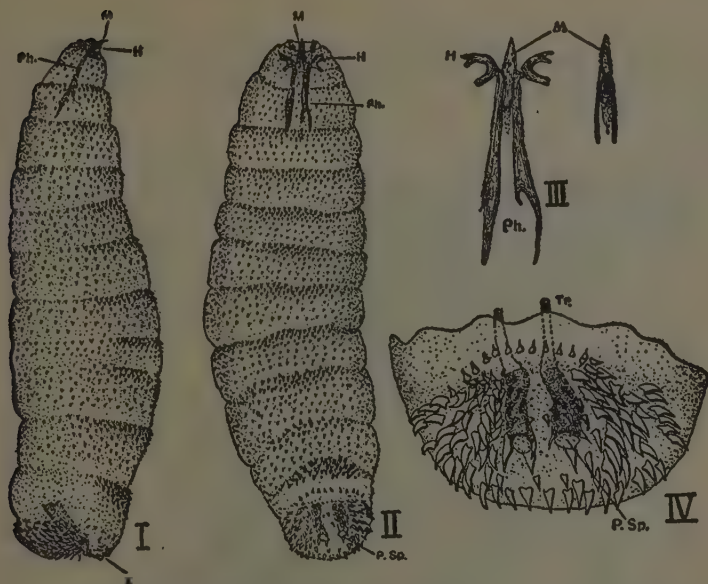


FIG. 9.—*Hypoderma bovis*: First-stage larva. I, Lateral view; II, ventral view; III, cephalopharyngeal skeleton with spine and mouth hooks; IV, caudal segment. Ph, Skeleton of pharynx; H, mouth hooks; M, spine; Tr, air tubes; P. sp., posterior spiracles (Carpenter and Hewitt)

Ventrally segments 2 to 9 are provided fairly constantly with a heavy band of spines along the posterior border, but it is not uncommon to find specimens in which segment 10 is also armed and others with segment 9 naked. The spines on the anterior borders of the segments, ventrally, vary even more, and usually end on the eighth or ninth segment. Laterally the armature is very irregular and rarely extends behind the sixth segment on the ventrolateral or the fourth segment on the mediolateral and dorsolateral areas. Dorsally the armature is almost entirely wanting. The greater part of the anal segment posteriorly is thickly covered with small spines surrounding the posterior spiracles, but the triangular spines are no longer present. The two posterior spiracles may be round or very irregular in outline. They consist of a group of circular rings or disks. The color of the stigmal plate is orange or yellowish brown, and the disks are separate or loosely connected in groups but always very distinct in individual outline. The number of disks varies from 12 to over 30, but usually with specimens collected in Texas it is from about 18 to 25 (fig. 14).

The fourth-stage larva of *H. bovis* is similar to that of *H. lineatum*, but when grown it is slightly larger. The only specific distinguishing characters that can be relied upon are the posterior stigmal plates. In *H. bovis* the stigmal plates are composed of disks or rings that are dark brown or black in color, and usually the whole group is closely fused together. The number of disks in *H. bovis* is usually considerably higher than in *H. lineatum*, running from 29 to above 40, with the normal number about 32 to 37 (fig. 15).



FIG. 10.—*Hypoderma lineatum*: Ventral view of first-stage larva. A, Mouth hooks; B, anterior spiracles; C, cephalopharyngeal skeleton; F, flattened spines on border of posterior spiracles; P. sp., posterior spiracles. × 121 (Laake)

FIFTH STAGE

The fifth or last larval stage of *H. lineatum* (fig. 16, *a-c*) tapers considerably toward the anterior extremity from about the eighth segment. The size of the larva varies from about 16 to 26 millimeters in length and from 7 to 11 millimeters in width. The surface is more rugged than in the preceding stages, especially on the sides. The spinous armature is heavy; and, although varying greatly with different specimens on the dorsal and lateral sides, it is constant

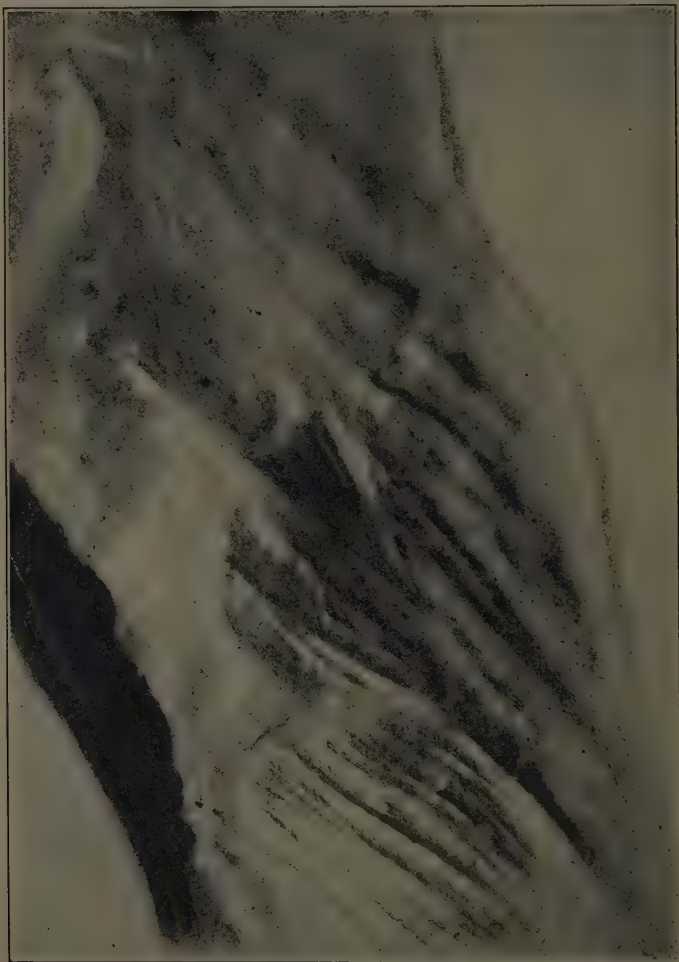


FIG. 11.—Second-stage larva of *Hypoderma lineatum* in submucous tissues of gullet.
Enlarged

ventrally on the posterior borders of segments 2 to 10, inclusive, and presents an excellent distinguishing characteristic for this species. The posterior stigmal plates are somewhat kidney shaped, flat, or slightly excavated toward the pseudostigmatic orifice, and have radiating furrows which are very distinct in the younger specimens (figs. 16, *d*; 17).

The fifth-stage larva of *H. bovis* is slightly larger, but otherwise very similar in shape to that of *H. lineatum*. The armature arrangement is similar to that of *H. lineatum*, except ventrally, where only segments 2 to 9, inclusive, are armed; very rarely a specimen is found with armature on the tenth segment and with a single or a few spines on the anterior border only. In *H. lineatum* there is always a fairly broad band of spines on the posterior border. The posterior stigmal plates of *H. bovis* are deeply excavated or funnel shaped toward the pseudostigmal orifice. This character is very reliable for distinguishing the species in this stage (fig. 18).

THE PUPARIUM

The puparium retains all the larval characters, except that it assumes a different shape and darkens in color to almost black. Its dorsal side is nearly straight and flat, with the anterior end plainly showing the operculum (fig. 16, d-f). The flat stigmal plates of *H. lineatum* and the funnel-shaped plates of *H. bovis* remain the same as in the mature larva and serve to distinguish the two species.

THE ADULT

The adult of *H. lineatum* (fig. 19) measures from 12 to 13 millimeters in length and has a wing expanse of from 23 to 25 millimeters. The female with ovipositor fully extended measures 17 millimeters in length. The general color of the adult is black, banded with yellowish and orange hair. The shade of the colors varies somewhat with different specimens and also changes according to the position and light in which the insect is viewed. The front, sides, and back of the head are covered with yellowish-white hairs.

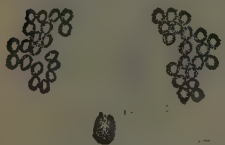


FIG. 14.—*Hypoderma lineatum*: Posterior stigmal plates of fourth-stage larva. Greatly enlarged (Laake)

The thorax is clothed with yellowish hairs except dorsally, where the posterior part of the prothorax and the mesothorax are more thinly covered with black and some yellow hairs. On this area

there are four distinct longitudinal lines which are nearly naked and shining. The basal segments of the abdomen are covered with grayish-yellow hairs, the middle segments are brownish black, and the terminal segments are clothed in orange-yellow hairs. The femora are black and the tibiae and tarsi brown. The entire legs are well covered with black and orange-colored hairs. The wings are slightly fuscous and the veins are dark brown to black.



FIG. 13.—*Hypoderma bovis*: Cephalopharyngeal skeleton and mouth hooks of third-stage larva. A, spine; B, anterior end, and C, posterior end, of mouth hooks. $\times 125$ (Laake)



FIG. 15.—*Hypoderma bovis*: Posterior stigmal plates of fourth-stage larva. Greatly enlarged (Laake)

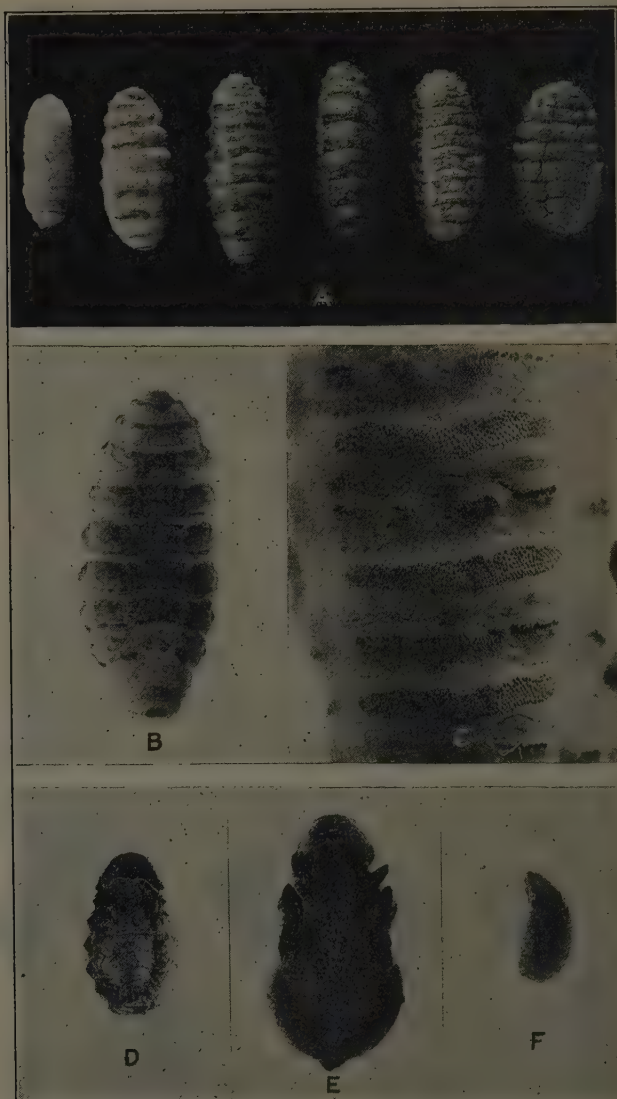


FIG. 16.—*Hypoderma lineatum*: a, Fifth-stage larvæ, newly molted to mature (ventral view, except mature larva, which is dorsal); b, fifth-stage larva, dorsal view; c, section of ventral side of mature larva; d, puparium after emergence of fly, dorsal view; e, ventral view of pupa; f, puparium, side view

The fly of *H. bovis* (fig. 20) is considerably larger and much stouter than that of *H. lineatum*. This is especially true of the thorax, which is much broader. The color is similar to that of *H. lineatum*, but the band of yellowish hairs across the prothorax dorsally is markedly wider and the shade slightly deeper than in *H. lineatum*. The shiny longitudinal lines of the thorax are obscured anteriorly by the hair. The color of the abdominal vestiture is similar to that of *H. lineatum* except on the terminal segments, which have a wider and more sharply defined band of lemon yellow, distinctly paler than in *H. lineatum*. The wing veins of *H. bovis* are of a reddish-brown color. The femora and the tibiae are black and well covered with black and yellow hairs, and the tarsi are brown and much less hairy than in *H. lineatum*.

HOW THE LARVÆ OF HYPODERMA LINEATUM GAIN ENTRANCE TO THE HOST

The method of ingress of various animal parasites is often a point of considerable economic importance. As has been indicated in the historical sketch, the opinions held by various investigators in regard to the way in which *Hypoderma* larvæ enter the host have been at wide variance; and even up to the present time there are but few who feel certain of the method of ingress of these parasites.

During 1916 plans were laid at the Dallas laboratory to carry out a series of tests to determine accurately the way in which the larvæ enter the host. These tests have been continued along similar lines up to date. Since a full knowledge of the habits of oviposition of adult *H. lineatum* has been gained, it is evident that there are really only two ways in which the larvæ might get into the host, one of these being by direct penetration through the skin and the other by being taken in by mouth in the egg or young larval stage.

The following plan, with slight modification, was carried out in all of the tests: Certain animals were placed in fly-proof cages and thus protected from all possibility of attack by heel flies during the season of fly activity. To these animals were administered by mouth the eggs of newly hatched larvæ. Most of these were applied to the tongue or inside of the lips of the host, but some were placed in capsules and the host made to swallow them. Certain of these animals were dissected at a time when the larvæ should be present in the gullets or other

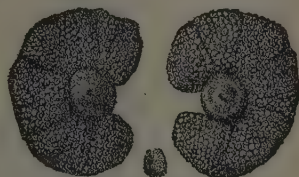


FIG. 17.—*Hypoderma lineatum*: Posterior stigmal plates of fifth-stage larva. Greatly enlarged (Laake)

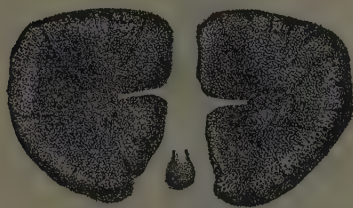


FIG. 18.—*Hypoderma bovis*: Posterior stigmal plates of fifth-stage larva. Greatly enlarged (Laake)

portions of the carcass commonly infested, to ascertain if possible whether any of them escaped from the digestive tract. Others were kept and watched the following fall, winter, and early spring for the appearance of larvæ in the subdermal tissues of the back. At the time that these animals were being fed with the larvæ and eggs, others were infested on the legs or elsewhere by allowing flies captured in nature or reared in cages to deposit eggs upon

them. These hosts were kept securely muzzled throughout the season when flies were likely to be about, except for the time that they were being fed, when they were placed in specially constructed stanchions which would not allow them to lick any part of themselves. The muzzles used were made of heavy wire, extending well up the nose and covered with closely woven ducking, except for two small holes above the nostrils.



FIG. 19.—Dorsal view of adult male of *Hypoderma lineatum*. Much enlarged.

As will be seen by reference to Table I, during 1917 three animals (Nos. 164, 169, and 176) were infested by allowing flies to oviposit on them. One of these received the eggs on the heels and thigh, another on the legs, shoulder, and neck, and the third on the back. In each of these a considerable number (45, 27, and 10, respectively) of grubs came to the subdermal tissue and cut holes through the skin of the back the following fall and winter. Another animal (No. 174) was given, by way of the mouth, 36 newly hatched larvæ and 82 eggs which were about ready to hatch. Nine of these larvæ were administered down the throat in a capsule. No grubs appeared on the back of this animal during the fall and winter, although it was shown that it was a favorable host by the fact that it had a good infestation during the previous year.

In 1918 three animals were used, two of these (Nos. 212 and 217) receiving infestations on the heels and one (No. 214) by way of the mouth. Both of those having eggs de-



FIG. 20.—Dorsal view of adult female of *Hypoderma bovis*. Much enlarged

posited on the heels developed grubs in the back. One had 45, with about an equal number on each side of the backbone, and the other had 2 when the animal was disposed of on December 23. Possibly other grubs would have come up later. The animals to which the young larvæ were fed was observed throughout the fall and winter and no larvæ whatever came to the back.

In 1919 11 animals were used in the tests. Four of these (Nos. 411, 412, 413, and 415) received eggs on the heels and front feet, one near the hips (No. 419), and three on the heels and elsewhere (Nos. 409, 410, and 414). Three (Nos. 416, 417, and 418) were fed eggs and newly hatched larvæ. One of those receiving eggs on the heels and elsewhere (No. 410) was killed shortly after the eggs began to hatch in an effort to determine the presence of larvæ in or under the skin. No larvæ were found but some small holes were clearly visible in the skin beneath one group of the eggs, and the connective tissue under the eggs was yellowish and edematous, just as it appears when the larvæ are present. On July 9, one of those animals which received eggs on the heels, front feet, hock, and side of abdomen (No. 409) was killed and examined; 76 larvæ were found along the gullet. One of the animals which received eggs on the heels and front feet (No. 411) was killed October 7 and no larvæ were found owing, it is believed, to the fact that the eggs were infertile. In the case of this animal no irritation or lesions indicating penetration were observed, after what should have been a normal period of incubation. All of the 112 eggs deposited on this animal were laid by one fly and some of the eggs clipped from the host and placed in an incubator failed to develop larvæ. Of the other three receiving eggs on the heels and front feet, all showed moderate infestations of grubs (average of 14.3) in the back the following fall and winter. The animal receiving the eggs on the hips only (No. 419) developed a total of 13 grubs the following winter, and the one having the eggs placed on the hock, front feet, and udder (No. 414) developed a total of 20. On the other hand, two of the animals (Nos. 417 and 418) which received fertile and well-incubated eggs, as well as healthy larvæ, by way of the mouth, failed to develop a single grub during the subsequent fall and winter. The third (No. 416) was killed July 9, and a careful dissection failed to reveal the presence of a single larva in the gullet or elsewhere.

In the tests begun in the spring of 1920 10 experimental animals were employed. Three of these (Nos. 167, 159, and 417) were infested on the legs, mostly on the hind ones from the hock down; one received eggs only on the top of the shoulders; two (Nos. 158 and 22) had the eggs placed on the front and rear legs and on the belly near the flank; and two (Nos. 160 and 414) received larvæ and eggs by way of the mouth. Two other animals (Nos. 92 and K23) were used to test the migratory tendencies of the second-stage larvæ, which were removed from the gullets of slaughtered cattle. These were inserted in pockets cut under the skin near the hock.

TABLE 1.—*Determination of method of ingress of Hypoderma lineatum into host*

No.	Animal	Age	Infested			Num- ber used	Results
			Date	Stage	Place and method		
164	Steer	7 months	1917 Mar. 7 to 14	Eggs	Heels and thigh	235	45 larvæ perforated skin on back Nov. 20 to Dec. 31.
169	Cow	6 years	Mar. 12 to 15	do	Legs, neck, and shoulder	220	27 had perforated skin on back Nov. 26.
174	do	3 years	Mar. 17 to 31	Larvæ and eggs	In mouth, naked 1 and in capsules.	118	No larvæ perforated skin on back.
176	do	2 years	Mar. 17	Eggs	On back	85	10 had perforated skin on back Dec. 20.
212	Cow	3 years	1918 Mar. 5 to 12	do	Heels	127	45 perforated skin on back Nov. 22, or before, to Jan. 8.
217	Steer	1½ years	Mar. 19	do	Heel	75	2 had perforated skin on back Dec. 23, when host was lost.
214	Cow	4 years	Mar. 18 to 29	First-stage larvæ	In mouth on tongue, naked 1	28	No larvæ perforated skin on back.
410	Steer	6 months	1919 Mar. 10 to 20	Eggs	Heels, abdomen, flank, and by anus.	186	Dissected Mar. 24. Holes in skin and induration beneath.
409	Bull	5 months	Mar. 10 to 16	do	Heels, legs, abdomen	168	July 9, slaughtered, 76 larvæ in gullet.
411	do	15 months	Mar. 17	do	Heel, front feet	112	Oct. 7, dissected, no larvæ found.
416	Cow	3 years	Mar. 20 to 22	Eggs and larvæ	In mouth, on tongue	80	July 9, dissected, no larvæ found.
417	do	2 years	Mar. 22 to Apr. 5	Larvæ, first stage	In mouth, on tongue, and inside lips	136	No larvæ perforated skin on back.
418	Heifer	1 year	Mar. 23 to Apr. 5	Eggs and first-stage larvæ	In mouth on tongue and lips	94	Do.
414	Cow	8 years	Mar. 16	Eggs	Feet, legs, and udder	62	20 perforated skin on back Nov. 17, or before, to Dec. 29.
415	do	3½ years	do	do	Feet	67	22 perforated skin on back Nov. 17, or before, to Dec. 4.
419	Heifer	1 year	Mar. 27	do	Each side near hip	77	13 perforated skin on back Nov. 19, or before, to Jan. 6.
412	do	2 weeks	Mar. 17 to 27	do	Heel, front foot	64	10 perforated skin on back Dec. 1, or before, to Dec. 23.
413	do	6 weeks	do	do	do	49	11 perforated skin on back Dec. 6 to Jan. 2.
160	Cow	4½ years	1920 Mar. 19 to 22	Eggs and first-stage larvæ	In mouth, naked 1	248	No larvæ perforated on back.
167	Heifer	1 year	Mar. 12	Eggs	Heels	200	3 perforated skin on back Nov. 21, or before, to Dec. 9.
163	do	do	Mar. 10 to 18	do	Top of shoulder	152	1 perforated skin on back Dec. 1.
159	do	2 years	Mar. 10 to 19	do	Heels	115	17 perforated skin on back Nov. 15 to Jan. 10.

414	Cow	9 years	Mar. 17 to 19	First-stage larvæ	In mouth, inside lips and on tongue, naked. ¹	70	Nov. 26 dissected and no larvæ found.
158	Heifer	2 months	Mar. 6 to 13	Eggs	Heels, belly, and near udder.	138	Oct. 25, killed by train, not examined.
417	Cow	3 years	Mar. 2 to 19	do	Hock and heel	280	Do.
K-23	Heifer	1 month	Dec. 22	Larvæ from gullet	Thigh under skin by incision	15	9 perforated skin on back Dec. 14-17, all to rear.
22	Bull	6 months	Mar. 22 to 28	Eggs	Heel and belly	340	July 3, dissected, 40 larvæ found.
92	Heifer	27 months	June 16	Larvæ from gullet	Hock, under skin by incision	60	32 perforated skin on back Nov. 21, or before, to Jan. 4.
92	Heifer	38 months	May 3	Larvæ from gullet	Under skin, hind leg	25	13 perforated skin on back Oct. 20, or before, to Nov. 28.
22D	do	1 month	Mar. 15 to 18	Eggs and first-stage larvæ	Right and left heels On skin right front foot.	160	8 perforated skin on back Nov. 9 to Dec. 24.
K-23	do	4 months	Mar. 3	Eggs	Left hock and foot	45	A apparently none hatched.
24-D	Calf	5 months	Mar. 16	do	Right heel and front foot	65	64 perforated skin on back Oct. 27 to Jan. 4.
160	Cow	5½ years	Mar. 29	First-stage larvæ	On skin, left hind foot	3	None perforated skin on back.
25-D	do	29 months	Aug. 26	Larvæ from gullet	Hind leg under skin	30	3 perforated skin on back Oct. 20, or before, to Oct. 27.
167	Heifer	30 months	do	do	Behind right ear under skin	26	15 perforated skin on back Oct. 17 to Dec. 11.
159	Cow	3 years, 5 months	do	do	Under skin on back	26	2 perforated skin on back Nov. 8 to Nov. 12.
167-1	Bull	5 months	do	do	Under skin hind leg	26	4 perforated skin on back Oct. 17 to Dec. 3.
418-1	do	1 month	Nov. 16	do	do	26	Oct. 17, dissected, 10 larvæ recovered.
25-D	Cow	3 years	Mar. 7	Eggs	Heels on hind legs	14	9 perforated skin on back Nov. 30 to Dec. 22.
K-23	Heifer	16 months	Mar. 7 and 8	do	Back and rump	80	26 perforated skin on back Nov. 1, or before, to Dec. 7.
418-1	Bull	5 months	Mar. 8 and 16	do	Hind heels	134	9 perforated skin on back Nov. 21, or before, to Jan. 2.
22-D	Cow	13 months	Mar. 8 to 16	do	do	131	Dipped in creosote dip; 1 perforated skin on back Dec. 4.
92	do	4 years	Mar. 10 to 25	First-stage larvæ	Placed on tongue	134	Dipped in derris solution; 1 perforated skin on back Dec. 14.
1	Horse	12 years	Mar. 15 and 16	Eggs	Rear and front heels and base of tail	89	None perforated skin on back.
160-1	Heifer	2 weeks	Mar. 20	First-stage larvæ and eggs	Placed on skin and hair, hind heels	175	Do.
167	Cow	3 years, 4 months	do	Eggs	Both rear heels	242	15 perforated skin on back Nov. 15, or before, to Jan. 12.
92-1	Bull	1 month	Nov. 14	Gullet larvæ	Under skin hind legs	35	Dissected Nov. 19, 15 recovered.
25D-1	do	3 weeks	Nov. 14 and Dec. 28	Larvæ from gullet	Under skin both hind legs	36	25 perforated skin on back Nov. 27 to Jan. 22.
25D	Cow	3¾ years	Dec. 28	do	Under skin right hind leg	29	8 perforated skin on side and back Jan. 7, or before, to Jan. 18.
92	Cow	4 years, 10 months	Jan. 4	Larvæ from gullet	Under skin right hind leg	21	14 perforated skin on leg, flank, and back Jan. 8 to Jan. 22.

¹ "Naked" means without use of a capsule or other covering.² Larvæ³ Eggs.

Of the three animals receiving the eggs on the legs, one (No. 417) was accidentally killed by a train during the late summer and no examination could be made. In November, larvæ first appeared under the skin on the backs of the other two cows (Nos. 167 and 159), and during the fall and winter one of them had 3 larvæ to reach the back, while the other had 17. With the animal infested on the shoulders (No. 163), a single larva appeared on the back during the following winter; but it had been observed that many of the eggs on this animal were infertile and had failed to hatch. One of the two animals with infestations on the legs and belly (No. 158) was also killed by a train and not examined, but the other (No. 22) was slaughtered and carefully dissected on July 3. A total of 40 second-stage larvæ were found on the viscera and along the gullet. One of the two hosts infested by way of the mouth (No. 414) was dissected on November 26 and no larvæ were found in the gullet or elsewhere. The other animal (No. 160) was observed carefully and repeatedly during the fall and winter and not a single larva came to the back. The two animals (Nos. K23 and 92) receiving the second-stage larvæ through incisions cut near the hock showed 9 and 32 larvæ, respectively. These appeared along the backs during the fall and winter.

During the spring of 1921 two heifers were infested by flies which deposited eggs on their hind legs. One of these (No. K23) received about 110 eggs on the feet, but apparently none of the 45 eggs hatched which were deposited on this animal on March 3. The first larva came to the back on October 27, and a total of 64 larvæ appeared during the winter. The other heifer (No. 22D) received far more eggs on the legs but developed only 8 larvæ on the back, the first appearing November 9.

During the season seven bovine hosts were infested by placing, in pockets cut under the skin, larvæ of *H. lineatum* removed from gullets of slaughtered animals. Two of the hosts (Nos. 92 and 160) were infested May 3 with larvæ (4.5 to 5.5 millimeters in length) inserted above the hock. Each developed an infestation in its back in the fall. The first larva reached the back October 20 or shortly before. Four cattle were infested with 26 gullet larvæ per animal on August 26; two received them in the right hind leg, one behind the ear, and one in the back about 8 inches behind the shoulder and 3 inches from the spinose processes; this was in order to compare the dates of appearance of larvæ on the back and the number successfully reaching that region.

One of the two hosts infested on the leg (No. 159) had larvæ present on the back on October 17, and at that time the other animal (No. 167-1) was killed and dissected. On a post-mortem examination 10 larvæ were recovered, 3 in the subdermal connective tissue of the back (but no holes had been cut through the hide), 1 under the spleen on the paunch, 1 on the paunch near the esophagus, 3 in the mesentery of the colon, and 2 in the submucous tissue of the gullet. One of the latter was near the paunch end of the gullet and measured 13.7 millimeters in length; the other was in the middle of the gullet and measured 11.6 millimeters. Both were headed toward the paunch.

In the case of the cow infested at the base of the ear (No. 25-D) the first larva reached the back October 17, and a total of 15 came to that region; with the cow infested on the back (No. 167) only two appeared (November 8 to 12). On November 16 a bull calf was infested in the hind leg by inserting in the skin 14 larvæ taken from the gullet of a slaughtered animal. These larvæ measured 11 to 15 millimeters in length and the first appeared on the back November 30. Nine of the 14 succeeded in coming to the back for normal development.

In the calf (No. 24-D) five first-stage larvæ were applied for a study of penetration. Although some of these were observed to penetrate the skin, none reached the back.

During 1922 seven cattle were used in the tests. One of these (No. 92) was protected from flies, but fed 89 newly hatched larvæ by placing them on the tongue and in the lips. In this animal not a single larva reached the back the following fall and winter. Of the other six hosts, five were infested on the heels and legs and muzzled to prevent ingress of newly hatched larvæ through the mouth. In all of these animals larvæ reached the back, the number per host varying from 1 to 26, despite the fact that two of the animals had the legs immersed in insecticides every day. The other animal (No. K-23), which received eggs on the back, developed nine larvæ in that region. The date of first appearance of larvæ in the subdermal tissue was not influenced materially by the date of infestation or by the point of ingress into the animal.

On November 14, 1923, 20 larvæ taken from the gullets of slaughtered cattle were placed beneath the skin by incision, on each of two calves (Nos. 92-1 and 25D-1). The point of introduction was about 6 inches above the hock joint on the outside of the right hind leg. The larvæ averaged slightly over 12 millimeters in length. On November 19 the older calf (No. 92-1) (1 month old) was dissected and 15 larvæ were recovered. Most of these were ranging upward in the connective tissue under the skin where there was marked infiltration, and one had passed between muscles on the rear of the thigh and was apparently following a large nerve, being only 3 inches from the spinal canal. In the other calf (No. 25D-1) 6 larvæ had reached the back and had perforated the skin, 4 on the right and 2 on the left side. On December 28 another lot of 16 larvæ from gullets were put under the skin of this calf on the left hind leg just above the hock. These were from 12 to 16 millimeters in length. Immediately preceding January 8, 12 grubs had reached the back and had punctured the skin. These were about equally distributed on each side of the spine; 7 others reached the back by January 22, making a total of 25. On December 28, 29 larvæ from 12 to 16 millimeters in length were introduced in an incision through the skin on the right hind leg of a cow, just above the hock. On January 7, or shortly before, the first larva appeared behind the right hip, and 7 others cut holes through the skin during the period up to January 18. One of these was only 7 inches above the point of introduction and the last one was on the left side just in front of the hip, a distance of about 33 inches from the point of introduction.

On January 4, 1924, 21 larvæ from 11 to 16 millimeters in length, from gullets, were introduced subcutaneously above the hock of another cow. On January 8 one larva cut through the skin $5\frac{1}{2}$ inches above the incision. On the following day 5 others punctured the skin, one of these being 30 inches above the point of introduction. The following day 3 others appeared, 1 of these being near the spinal column on the right side about 7 inches behind the shoulder, a distance of 40 inches in a line from the incision. A total of 14 grubs perforated the skin, all being on the right side.

It appears from these tests that when larvæ which are ready to leave the gullet are introduced subcutaneously they may not travel far from the point of introduction before puncturing the skin, and that they appear to pass upward under the subdermal connective tissue without penetrating deeply into the tissues as occurs when young larvæ from the gullet are introduced.

To recapitulate, in the tests carried out at the Dallas laboratory, 28 animals were infested by allowing flies to oviposit on the legs and bodies and were prevented from reaching any part of their bodies with tongue or mouth. Of these 28 animals, 2 were accidentally killed and not examined. In one of those slaughtered for dissection no larvæ were found, but in this case no hatched eggs were observed on the animal and other evidence indicated that none of the eggs placed upon it were viable. One of the other animals was killed immediately after the eggs hatched and, although no larvæ were found, there were strong indications of the penetration of larvæ through the skin. Two of the other animals killed showed an abundance of grubs along the gullet and on the viscera. Twenty of these animals were kept for observation during the fall and winter, and in every one of them grubs came to the back during the normal grub season. In all of the 11 cattle which were infested by introducing larvæ from the gullets of slaughtered cattle under the skin on the legs, behind the ear, and on the back, larvæ appeared under the skin at the usual time during the following fall and winter. Larvæ were also recovered in 2 animals which were dissected after larvæ had been introduced under the skin in this way. On the other hand, among the 8 animals to which larvæ and eggs were given by mouth, neither of the 2 which were carefully dissected showed the presence of larvæ, and in not a single instance among the 6 cattle held for observation did a grub appear along the back.

In 1922 Carpenter, Phibbs, and Slattery (19) report similar results in experiments carried out in Ireland. No grubs were recovered in calves to which numerous larvæ were fed but heavy infestations developed in carefully muzzled calves exposed to the oviposition of flies.

The fact that the larvæ penetrate through the skin is established by the following evidence:

- 1.—The eggs are usually laid on the hairs comparatively close to the skin, which would favor penetration. They are firmly attached and the eggshells, after the larvæ have escaped, remain attached to the hair.

- 2.—The eggs are not fitted with an operculum as in the case of the horse bots, the ends merely splitting as the larvæ emerge.

3.—It is not necessary to apply friction to the eggs to cause them to hatch, as the larvæ have been observed in many instances by the writers and others to crawl from the shells when their development was completed, provided the proper temperature was maintained.

4.—Much skin irritation in areas where eggs have been attached to the hairs is in evidence about four days after the eggs have been deposited. It has been observed repeatedly that violent stamping, kicking, and licking of the affected parts by the host occur soon after the hatching of the eggs begins, and a few days later soreness and the formation of scabs due to the exudation and hardening of serum are apparent. When these scabs are removed, a cluster of hatched eggs is usually found attached to the hair in their midst. (Fig. 21.)

5.—The actual penetration of a number of larvæ soon after hatching has been observed by the writers and their associates. This process will be described later.

6.—Stub (95) has been able to trace the route pursued by young larvæ from the inside of the right tibia over the shoulder and around the muscles of the neck to the connective tissue of the esophagus.

Taking the evidence set forth herein and considering the observations of other investigators whose work entirely corroborates it, there seems now to be no doubt that the normal method of ingress for the larvæ of both *H. lineatum* and *H. bovis* is directly through the skin at the point where the eggs are attached, and proves that there is comparatively little likelihood of infestation occurring by means of larvæ taken in by the mouth. It is desirable to stress at this point the demonstration given, by the slaughtering of some of the animals as above outlined, that the larvæ entering cattle through the skin on the lower legs may be found in the gullet in considerable numbers during the succeeding months. This proves the fallacy of the suggestion frequently made by investigators that those larvæ which are found in the gullet were probably taken in by the mouth and that they may perish and never reach the back. It should be noted that the writers have shown herein that larvæ of *H. lineatum* removed in the second instar from the gullets of cattle and introduced under the skin of uninfested bovines will not only appear under the skin on the backs of the new hosts in the proper season, but may and probably usually do pass again into the body cavity and even return to the gullet before going to the back.



FIG. 21.—Scab removed from a lesion on a cow, caused by penetration of newly-hatched larvæ of *Hypoderma lineatum*. Note the three hatched eggs on the hair

DEVELOPMENT AND HABITS

NUMBER OF EGGS ON HAIR

The eggs of *H. lineatum* are usually laid in a series of from 5 to 12 and occasionally as many as 20 may be attached to a single hair. The

number depends to some extent upon whether the fly is disturbed during the process of oviposition and also upon the length of the hair. In the case of *H. bovis* the eggs are always deposited singly on the hair.

DISTRIBUTION OF EGGS ON HOST

H. lineatum shows a marked tendency to oviposit on the heels of cattle which are standing, the favorite place apparently being the short hair overhanging the rear of the hoof and between the hoof line and the dewclaws. Many eggs, however, are deposited higher on the legs in the region of the hocks and a few above the hock line. Some eggs are also deposited on the belly, flanks, and forelegs, and occasionally on the sides, shoulders, and neck. In practically all of the writers' observations of depositions on cattle which are not lying down, it seems evident that many of the eggs deposited elsewhere than on the heels are laid after the fly has been disturbed by the actions of the host. Many eggs are also deposited along the escutcheon, on the outside of the thighs, on the tail, and on the base of the udder, and some along the side and on the forelegs in the region of the elbow joint. Infestations in these regions are especially common among quiet stock, oviposition taking place while they are lying down. In one instance over 200 fresh eggs were found attached to the hair on an area not over 2 inches square just behind the upper end of the scapula. The writers' observations on flies in nature and upon those placed on hosts in captivity indicate that they prefer the short, comparatively coarse hairs to the long, dense, silky ones.

H. bovis also prefers the heel or lower leg for a place of attachment for its eggs, but since this species frightens the animals much more, and since the flies continue to follow the cattle, depositing eggs while pursuing the rapidly running animals, a much larger percentage of eggs is deposited higher on the legs, especially in the region of the thighs and on the rump. Although a considerable number of eggs are laid on other parts of the body, especially along the sides, they tend to be concentrated on the hind quarters.

METHOD OF ATTACHMENT OF EGGS

As has been indicated under its description, the egg is provided with a definite attachment area or clamp. In addition to the placement of the clamp around the hair, each egg appears to be provided with a cement which when dry firmly glues it to the hair. Eggs have been observed to remain attached on the host for several weeks, sometimes the distal end gradually breaking away so as to leave only a portion of the shell. As shedding of the winter coat usually takes place about the time the eggs are deposited, many of them are shed off and perish before they have had an opportunity to hatch.

The eggs are nearly always attached very close to the skin, and this renders them inconspicuous, as they are usually covered by the overhanging hair. This is particularly true of *H. bovis*.

INCUBATION

The incubation period of *H. lineatum*, as observed in many lots of eggs kept under varying conditions, was found to range from

64 hours to 10 days. It is evident that the period of incubation is markedly affected by temperature. With eggs deposited on a host this would vary according to their proximity to the skin and the insulation from air temperatures by the hair. With normally placed eggs the basal ones on the hair are usually very close to the skin, but in the case of eggs deposited on fairly long hair the distal ones may be half an inch away from the skin.

Table 2 sets forth a number of observations on the period of incubation of eggs of *H. lineatum*. Many of the records are only approximate, the time of hatching having been determined largely by the irritation of the host produced by penetration of the larvæ. It will be observed that in one instance irritation was evident approximately $2\frac{3}{4}$ days from the time the eggs were deposited on the legs of a calf. This incubation period was almost exactly the same as that observed on a portion of the same batch of eggs placed in an incubator at approximately 98° F. The writers' observations indicate that the usual incubation period on the host is from 3 to 6 days, probably most of the eggs hatching toward the end of the third day and early in the fourth.

TABLE 2.—Incubation of eggs of *Hypoderma lineatum* in situ and in incubator at Dallas, Tex.

Deposited	Number of eggs	Place and method	Date of hatching	Incubation period	Air temperature		
					Maximum	Minimum	Mean
1917							
Mar. 7, 4.30 p. m.	100	Calf's leg	Mar. 11 ¹	Days 4—	° F. 84	° F. 30	° F. 65.6
Mar. 8, 4.30 p. m.	20	do.	do.	3—	84	30	63.4
Mar. 14	175	Incubator	Mar. 15-18	3+	87	85	86
Mar. 23 ²	100	do.	Mar. 25	2+	87	85	86
1918							
Mar. 16 ²	160	do.	Mar. 18, a. m. to p. m.	2+	97	96	96.5
Mar. 26, p. m. ²	20	do.	Mar. 29, a. m.	2¾+	99	97	98
1919							
Mar. 10	65	Calf's leg	Mar. 16 ¹	6—	77.5	37.5	60.5
Mar. 10, 5 p. m.	175	Calf's belly	do.	6—	77.5	37.5	60.5
Mar. 12 ²	40	Vest pocket and incubator.	Mar. 22 to 24	10+	81	37.5	62.7
Mar. 14 ²	40	do.	Mar. 22	8+	81	40.5	63.8
Mar. 16, p. m.	60	Cow's legs and body	Mar. 20 ¹	4—	79	40.5	61
Mar. 19, 5 p. m.	100	Incubator	Mar. 22, 2.30 p. m., to Mar. 23, 11 a. m.	3 to 4	90	90	90
Do.	25	Calf's belly	Mar. 22	3	81	40.5	63.2
Do.	37	Calf	Mar. 22, p. m.	3—	81	40.5	63.2
Mar. 20, 1 p. m.	3	On calf and in incubator.	Mar. 24	4—	90	90	90
Mar. 21, 11 a. m. ²	231	Incubator	Mar. 23, 7 p. m. to Mar. 24, a. m.	2-3+	90	90	90
Mar. 27, 2.30 p. m.	260	do.	Mar. 30, 6 p. m. to 10 p. m.	3+	90	90	90
Mar. 27, p. m.	77	Cow's body	Mar. 31, p. m.	4—	93	35.5	60.3
Do.	7	Calf's leg	Mar. 31 ¹	4—	93	35.5	60.3
1920							
Mar. 6, 4 p. m.	80	Calf's heel and belly	Mar. 9, 5 p. m. ¹	3—	55	20.5	38
Do.	200	Calf at hock	Mar. 9, p. m. ¹	3—	55	20.5	38
Mar. 10, 5 p. m.	52	Calf's shoulder	Mar. 15, a. m., ¹ one-half hatched.	4½—	76	36	61.1
Mar. 12, 5 p. m.	200	Calf's heels	Mar. 16 ¹	4—	76	36	61
Mar. 13, 5 p. m.	100	Calf's shoulder	Mar. 22, a. m. ¹	3½—	81.5	42	63.4
Mar. 22, 5 p. m.	250	Calf	Mar. 26 ¹	4—	80	46	61.7
Mar. 28, 5 p. m.	95	Calf's legs and belly	Mar. 31, 6.30 p. m., to Apr. 1, 3.15 a. m.	3-3.5	90	40	63.7

¹ Hatching determined by the kicking and rubbing of host, some checked by actual examination.

² Collected from animals infested under natural conditions. Exact time of deposition unknown.

TABLE 2.—Incubation of eggs of *Hypoderma lineatum* in situ and in incubator at Dallas, Tex.—Continued

Deposited	Number of eggs	Place and method	Date of hatching	Incubation period	Air temperature		
					Maximum	Minimum	Mean
1921				Days	° F.	° F.	° F.
Mar. 15, 11.30 a. m.	70	Incubator	Mar. 18, 9 a. m. to p. m.	3—	98	98	98
Do	155	Calf's feet	Mar. 18, 9 a. m. ¹	3—	87	63.5	74.6
Mar. 16, 5 p. m.	40	Calf's leg	Mar. 19, a. m. ¹	2½—	87	63.5	74.5
Do	16	Incubator	Mar. 19, 9 a. m. to 12 m.	2½—	98	98	98
1922							
Mar. 15, 4.15 p. m.	15	Incubator	Mar. 18, 1 to 2 p. m.	3—	90	90	90
Mar. 16, 2.30 to 2.45 p. m.	45	do	Mar. 19, 10 a. m. to 4.40 p. m.	3	90	90	90
Mar. 20, 12.50 to 1.10 p. m.	85	Cow's heels	Mar. 24, 10.30 a. m.	4—	84	36	64.8
Do	74	Incubator	Mar. 23, a. m. to p. m.	3	90	90	90
Mar. 15, 3.13 to 3.15 p. m.	32	do	Mar. 18, 11 a. m. to 1 p. m.	3—	90	90	90
Mar. 28, 3.15 to 3.30 p. m.	72	do	Mar. 31, 8 a. m. (before) to 8.15 a. m.	2½	90	90	90

¹ Hatching determined by the kicking and rubbing of host, some checked by actual examination.

Glaser (29), without making it clear whether he is dealing with *H. bovis* or *H. lineatum*, states that he has observed the incubation period of eggs clipped from the host to be 12 days. He also says that on living animals development is completed in less than 3 full days. Hadwen (36), basing his statements on observations in Canada, states that the eggs when removed from the host hatch in about 7 days, the shortest period being from 4 to 5 days, but apparently he made no observations on the incubation of eggs on the host.

The writers have made few exact observations on the incubation period of *H. bovis*. At Middletown, N. Y., 2 out of a lot of 6 eggs deposited on a calf June 8 at 3.30 p. m. had hatched on June 11 at 12.15 p. m., a period of approximately 3 days. These were left on the host. In one instance in which eggs were sent by mail from a northern State to the Dallas laboratory and placed in an incubator they hatched in less than 7 days after collection. Carpenter (17) observed eggs attached to a host to be hatched in slightly less than 4 days.

The writers, in their work with reared flies, have obtained a considerable number of eggs from females which were not associated with males, and in none of the cases was there any hatching, indicating that parthenogenesis does not occur in this species. The percentage of viable eggs deposited by fertilized females seems to vary considerably. In some instances a hatch of almost 100 per cent has been observed, whereas in other cases the examination of a series of eggs showed a hatch of less than 50 per cent. It seems certain that the percentage of the hatch is higher when the eggs are deposited and allowed to remain on a host than when they are removed and placed in an incubator, although in a few instances a hatch of above 90 per cent was obtained among eggs kept in an incubator.

In general it appears that the eggs attached lowest on a hair hatch slightly earlier than those toward the distal end. When this

occurs it is probably due to the fact that the lower eggs, being closer to the skin, are kept at a slightly higher temperature.

Several hours before hatching, the segmentation and rows of spines are distinctly discernible through the shell. The larva becomes active shortly before hatching and can be observed through the eggshell pressing the mouth parts forward against the end of the egg. Finally the suture across the end of the egg is ruptured and the larva crawls out rather rapidly.

LARVAL ACTION AFTER HATCHING

The larva of *H. lineatum* after hatching usually crawls directly down the hair which bears the egg and after feeling about with the mouth parts begins to burrow directly into the skin at the base of the hair. The body is usually more or less extended along the hair, and during the initial efforts there is considerable twisting, expansion, and contraction. After the first few segments have been worked into the skin the larva becomes more quiet. The burrowing is slow but usually rather steady in case of vigorous specimens. Progress is retarded as the middle body segments reach the surface of the skin, and usually it is slightly accelerated when the larva has become almost completely imbedded. The time occupied for a larva to disappear after it has begun burrowing has been observed to be about one and one-half hours and sometimes considerably longer.

In nature it appears that several larvæ frequently enter the host through the same hole, and this no doubt greatly facilitates the penetration after the first larva has gained entrance.

Considerable difficulty was experienced in watching the penetration of the larvæ into the skin, mainly owing to the difficulty of holding a host quiet for considerable periods of time but also to the fact that the larvæ, on account of their small size and delicate structure, are very easily lost sight of. Most of the writers' observations on penetration were made with freshly hatched larvæ taken from an incubator. Even with the most careful handling there was a high mortality, apparently much greater than when the eggs are attached to the host in the natural way. It was observed repeatedly that larvæ removed from an incubator and placed on hair would wander about for a time before attempting to burrow and in so doing it seemed that they became more sensitive to drying, probably through the rubbing off of the gelatinous material with which their bodies are covered when they first emerge from the egg. Many larvæ put on hosts in this manner began burrowing, but perished during the process. In making observations a calf was usually placed on a table and firmly held or even strapped down so that the actions of the larvæ could be followed under hand lenses or binoculars. Where the hair had been clipped closely, early tests with the penetration of larvæ through the skin were unsuccessful, and all subsequent observations on penetration were made on hair one-fourth inch long or longer. In order to reduce the chances of escape without detection, it was the usual practice to clip closely or shave a narrow area around a tuft of hair and to place the larvæ upon this tuft.

Several attempts were made to observe the penetration of larvæ on the hands or arms of man. Usually the larvæ were watched

for periods of from 10 to 30 minutes, but they were not allowed to remain indefinitely. Although some of the larvæ made slight attempts to penetrate into hair follicles, in no case did they succeed in making much progress. In one instance a number of larvæ were placed on the conjunctiva of the eye of a rabbit. They moved about actively for some time and could be seen for an hour or more in the conjunctival region, but apparently they made no effort to penetrate, and produced only a very slight irritation to the eye.

The writers have made no observations on the penetration of larvæ of *H. bovis*, but have frequently observed the lesions produced by the burrowing of this species.

In 1914 (17) Carpenter, Hewitt, and Reddin recorded observations on the penetration of *H. lineatum* through the skin of cattle at points where eggs were attached. In addition to finding lesions at those points they succeeded in squeezing from the penetration holes along with serum a newly hatched maggot of this species. In the same publication the authors record observations on the penetration of first-stage larvæ of *H. bovis*, stating that it required about six hours for them to get into the skin. Prior to this Glaser (29) had failed in attempts to get the young larvæ to penetrate through the shaven skin, but in one case previously mentioned the larvæ penetrated through the skin on his own leg. The time occupied from the detection of the presence of the larva until it had disappeared was one and three-fourths hours.

In 1916 (33) Hadwen published a number of observations on the action of larvæ, both on living hosts and on pieces of skin freshly cut from cattle. He failed to observe the penetration of larvæ on living animals, but in a number of tests on hide removed from a bovine he observed larvæ to burrow partially, and in a few cases completely out of sight.

LESIONS PRODUCED BY THE PENETRATION OF FIRST-STAGE LARVÆ

The presence of exudate and pimples on cattle immediately under the eggs of *Hypoderma* from which the larvæ had emerged was first recorded by Carpenter, Hewitt, and Reddin in 1914 (17). Hadwen (33) has rather fully described the skin lesions of the two species of *Hypoderma*. He proposes the name "hypodermal rash" for the condition resulting from larval penetration.

When the newly hatched larvæ have burrowed into the skin and when their posterior segments are about flush with the skin surface there begins to appear a watery secretion, presumably blood serum. After the larva disappears this exudate increases in quantity and several hours later small pimples form which in some instances, at least, have been found to contain pus. In the case of *H. lineatum* where a number of larvæ often penetrate near one another, the inflammation and exudate become more marked and often the hair is matted, making a scab. With *lineatum* this irritation is often very marked, the entire area near where the penetration occurs becomes swollen, and in certain instances where a large number of larvæ have penetrated the heels of a calf the hind leg from the hock down has been observed to be swollen. These swollen areas are more apparent when large numbers of eggs are de-

posited along the back of the thighs, on the escutcheon (fig. 22), or on the base of the udder. A number of instances have been observed where the soreness and swelling extended down the rear quarters to the udder and the tenderness made milking difficult.

Beneath the skin these swellings are similar in appearance to the "licked-beef" condition ordinarily found along the back when the last-stage larvæ reach that region. The connective tissue around the point of penetration is edematous, tinged with yellow, and sometimes slightly bloody.

The scabs become dry within a few days and can be removed. Usually a small quantity of hair comes off with them and a number of pits are left in the skin indicating the points where the larvæ have penetrated. If the scabs are not removed artificially they disappear in the course of a week or two. Animals slaughtered during the period of larval penetration have the hides more or less damaged at points where the larvæ penetrate, and slight infiltrated areas are visible on the carcass.

As has been stated by other writers, these lesions may serve as portals through which disease organisms, such as anthrax or tuberculosis, may enter.

The actions of the animals at the time the larvæ penetrate have been mentioned in a general way. The first inclination of an animal, after penetration on the heel begins, is to shake the foot. This is usually followed by licking (fig. 23), which is often very vigorous and prolonged, and animals have been observed to continue it for two minutes without stopping. When the individuals are not allowed to lick the heels they usually twist, squirm, kick, and stamp, thus showing marked pain or irritation.

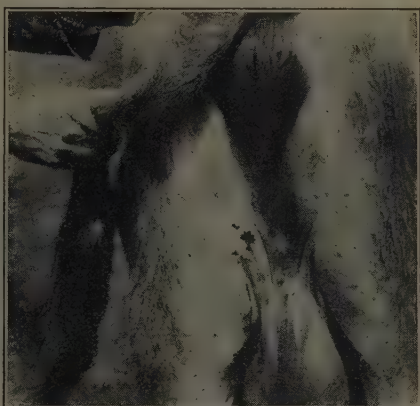


FIG. 22.—Lesions on escutcheon of cow, caused by penetration of newly-hatched larvæ of *Hypoderma lineatum*

OCCURRENCE IN THE GULLET AND BODY CAVITY

On account of the minute size and translucent appearance, it is not surprising that various investigators have been unable to observe the course followed by the first-stage larvæ after penetration of the skin. Stub (95), working in Copenhagen, has given us the only definite record. In a post-mortem he observed an infiltrated area in the superficial connective tissue on the inside of the right tibia, and succeeded in following the track over the shoulder, around the muscles of the neck to the tissue on the esophagus, where it enters the thoracic cavity. Here he found a number of larvæ in close proximity and measuring 1 to 2 millimeters in length. Hadwen (40)

has observed the tracks of the larvæ up the tendons to the knees or hocks in the elbow and patellar regions and in some cases farther up the legs; no larvæ, however, were recovered in these regions.

For many years it has been known that larvæ of the genus *Hypoderma* are found in considerable numbers in the connective tissue between the mucous lining and the muscular coat of the gullets of cattle. Since one of the writers (57) has found a method of determining accurately the species of the larvæ in any stage of their development, numerous collections of specimens have been examined from the gullets of cattle in regions where *H. bovis* occurs plentifully, and only one specimen of that species has been found. These observations involved the examination of 1,140 larvæ removed from the gullets of 563 cattle, and during every month of the year when they were found to be present in that part of the host. It is safe to conclude from these observations that the larvæ of this species do not have the habit of going to the gullet and spending some time



FIG. 23.—Cow licking heel where larvæ of *Hypoderma lineatum* are penetrating

there as occurs with *H. lineatum*. The single larva of *H. bovis* found in a gullet was taken at Chester, N. Y., on December 19, 1922. It was 10 millimeters long and was found lying loose on the tissue at about one-fourth the length of the gullet from the pharynx.

Since it appears that *H. bovis* does not frequent the gullet it may be taken for granted that all, or practically all, of the published statements of the occurrence of *Hypoderma* in the gullet appertain to *H. lineatum*, and the following discussion relates to that species only:

The principal data appertaining to the occurrence of the larvæ in the gullets are given in Tables 3 and 4. It will be observed that there is a gradual increase in the average size of the larvæ from their first appearance to their migration from the gullet. The range in sizes is observed by the writers to be from 1.5 to 16.9 millimeters. Among the larvæ found in the gullet only a small percentage are in the third stage, the others being in the second. Hadwen (40) reports finding in the submucosa of the gullet of a heifer a larva at least 2 millimeters long which he considered in the first stage.

TABLE 3.—*Number, size, and direction of travel of larvæ of Hypoderma lineatum in each of 10 divisions of gullets of cattle examined during each month at Dallas, Tex.*

	March	April	May	June	July	August	September	October	November	December	January	Total
Number of larvæ headed toward pharynx and paunch in each of 10 divisions of the gullet from pharynx to paunch:												
First—												
Pharynx.....	0	2	1	1	10	10	14	5	4	0	0	47
Paunch.....	0	3	0	1	4	6	16	4	4	1	0	39
Second—												
Pharynx.....	0	6	0	1	5	16	18	11	10	0	0	67
Paunch.....	1	2	1	0	5	13	15	7	6	1	0	51
Third—												
Pharynx.....	1	1	0	0	8	26	14	13	8	0	0	71
Paunch.....	0	2	0	2	13	21	27	14	16	2	0	97
Fourth—												
Pharynx.....	2	1	0	0	17	35	23	14	22	1	0	115
Paunch.....	0	2	1	1	4	22	30	12	16	4	0	92
Fifth—												
Pharynx.....	0	2	2	0	15	29	30	21	30	1	0	130
Paunch.....	0	0	0	5	8	25	35	16	25	3	0	117
Sixth—												
Pharynx.....	0	8	5	3	15	36	41	19	22	2	0	151
Paunch.....	1	4	3	3	16	31	41	20	16	7	0	142
Seventh—												
Pharynx.....	1	4	9	1	24	42	39	22	25	4	0	171
Paunch.....	0	9	5	4	14	49	34	10	21	5	1	152
Eighth—												
Pharynx.....	1	16	7	6	33	60	32	21	22	2	0	200
Paunch.....	3	21	7	3	31	49	50	12	24	6	0	206
Ninth—												
Pharynx.....	3	8	10	4	26	70	41	17	22	1	0	202
Paunch.....	1	12	8	2	32	65	52	20	31	3	0	226
Tenth—												
Pharynx.....	2	2	6	2	26	43	43	9	18	3	0	154
Paunch.....	2	4	3	2	17	48	37	11	16	1	0	141
Total number of larvæ headed toward—												
Pharynx.....	10	50	40	18	179	367	295	152	183	14	0	1,308
Paunch.....	8	59	28	23	144	329	337	126	175	33	0	1,126
Grand total.....	18	109	68	41	323	696	632	278	358	47	0	2,434
Length of larvæ (millimeters):												
Minimum.....	2.6	1.5	3.4	(1)	3.6	3.8	6.0	6.0	8.0	9.6	12.0	-----
Maximum.....	4.9	6.9	5.2	-----	12.4	14.0	15.5	15.9	16.9	15.8	12.0	-----
Average.....	3.98	3.7	4.4	-----	6.7	7.4	10.3	11.9	12.9	13.4	12.0	-----
Number of gullets examined.....	33	119	21	8	30	60	29	22	46	182	146	697
Average number of larvæ per gullet.....	0.55	0.92	3.24	5.13	10.77	11.60	21.79	12.64	7.78	0.26	0.01	3.69

(1) Larvæ not measured.

By reference to Table 3 it will be seen that throughout the season the majority of the larvæ occurred in the paunch half (last five divisions) of the gullet, the percentage of the total number in this half being 67.87. It was hoped that some indication of the place of entrance into and exit from the gullet might be given by a study of the position and direction of travel of the larvæ during different seasons but one can draw no definite conclusions from an analysis of the figures. During the first five months the number of larvæ heading toward the pharynx was greater than the number heading toward the paunch. This, together with the fact that 76 per cent of the larvæ present during the first 5 months of infestation were in the lower half of the gullet clearly indicates that the larvæ do not enter the gullet at the pharynx end. The evidence, however,

is not clear that the larvæ enter or leave the gullet tissue at the paunch end. It is possible that some of them reach the connective tissue by penetrating the muscle along the sides of the gullet. The writers' observations indicate that there is considerable variation in the size of the larvæ at the time they reach the gullet, and that the larvæ continue to reach the gullet over a much longer period than is covered by the entrance of the larvæ into the host.

TABLE 4.—Number, size, and direction of travel of larvæ of *Hypoderma lineatum* in each of 10 divisions of gullets of cattle examined during each month in New York State.

Month	June	July	August	September	October	November	December	January	February	March	April	May	Total
Number of larvæ headed toward pharynx and paunch in each of 10 divisions of the gullet from pharynx to paunch:													
First pharynx	0	0	6	0	2	0	2	2	1	0	0	0	13
First paunch	0	0	7	1	0	0	0	1	0	0	0	0	9
Second pharynx	0	0	5	2	2	0	3	1	3	0	0	0	16
Second paunch	0	0	5	0	1	0	1	1	2	1	0	0	11
Third pharynx	0	0	3	1	6	0	0	2	3	0	0	0	15
Third paunch	0	0	4	1	3	0	1	0	0	0	0	0	9
Fourth pharynx	0	0	2	3	7	0	2	4	4	5	0	0	27
Fourth paunch	0	0	4	2	7	0	2	5	6	0	0	0	26
Fifth pharynx	0	0	1	3	17	1	8	2	1	0	0	0	33
Fifth paunch	0	0	3	6	14	3	4	5	0	0	0	0	35
Sixth pharynx	0	1	0	6	17	0	1	6	7	2	0	0	40
Sixth paunch	0	0	11	3	25	0	4	7	8	2	0	0	60
Seventh pharynx	0	0	8	14	18	0	2	12	9	2	0	0	65
Seventh paunch	0	0	8	6	22	0	3	4	8	3	0	0	54
Eighth pharynx	0	0	16	11	19	0	2	17	5	1	0	0	71
Eighth paunch	0	0	11	10	37	0	1	9	6	2	0	0	76
Ninth pharynx	0	1	15	14	22	0	0	20	14	1	0	0	87
Ninth paunch	0	2	17	8	48	0	1	15	11	2	0	0	104
Tenth pharynx	0	2	14	7	23	0	0	19	7	1	0	0	73
Tenth paunch	0	1	14	5	46	0	1	25	9	1	0	0	102
Total number of larvæ headed toward—													
Pharynx	0	4	70	61	133	0	13	91	55	13	0	0	440
Paunch	0	3	84	42	203	0	17	71	55	11	0	0	486
Doubtful	0	0	7	1	0	1	3	2	8	3	0	0	25
Grand total	0	7	161	104	336	1	33	164	118	27	0	0	951
Length of larvæ (millimeters):													
Minimum	3.5	3.0	3.0	4.0	5.0	7.3	6.5	8.7	10.0				
Maximum	4.0	6.0	7.3	8.0	5.0	11.1	14.7	14.9	15.6				
Average	3.82	4.62	5.52	6.08	5.58	6.99	9.97	12.13	13.65				
Number of gullets examined	15	61	68	28	25	15	21	27	72	88	5		440
Average number of larvæ per gullet	0.11	2.37	3.71	13.44	0.71	1.57	6.07	1.64	.31	0			0.216

Table 4 presents some of the data obtained during the examination of gullets in several localities in New York. Most of them were taken from cattle kept in the vicinity of Ithaca, Chester, Albany, and Buffalo. The combining of the records obtained in several different localities makes the figures more irregular than those obtained at Dallas. The figures show that about 77 per cent of the larvæ were found in the posterior half of the gullet. It will be noted that there is considerable irregularity in the average number of larvæ per gullet, there being a marked decline in the number in November and December, where it seems almost certain from analogy that the maximum should have occurred. The low average in these two months can be explained by the fact that the gullets were taken from a very few lots and were probably from a very small number of herds of cattle. It is well known that the extent of infestation varies in different herds.

The occurrence of larvæ, varying considerably in size, on the surface of various abdominal organs has been noted by a number of investigators. For instance, Koch (53) records having found larvæ on the pleural side of the gullet as well as under the mucous coats; on the surface of the spleen; some on the paunch and one between the muscular and mucous layers of it; a few among the intestines; and some in the connective tissue of the thoracic cavity just below the vertebral column. Horne (45) has on several occasions observed several larvæ in the connective tissue around the kidneys, and Hadwen and Fulton (40) have observed several larvæ on the pericardium. Berg (3) has found larvæ in the connective tissue between the small loin muscles and the muscle of the hip, and Koch (53) has observed a single larva in the inter-muscular tissue of the back. Many writers have recorded the finding of larvæ, sometimes in considerable numbers, in the spinal column throughout the greater portion of its length and also passing through the posterior foramina. Hadwen and Bruce (38) state that larvæ observed by them in the spinal canal were found in the areolar tissue which surrounds the dura mater. Their presence was accompanied by evidences of green pigmentation and gelatinous infiltration at different points along the cord.

In the writers' own work they have encountered larvæ in nearly all of the locations where they have been reported by others. It is



FIG. 24.—*Hypoderma lineatum*: Diagram showing position, direction of travel, and length of larvæ in millimeters in gullet of calf (No. 22)

not at all uncommon for the larvæ to be present just under the pleura along the esophagus. The larvæ found in that region were practically of the same size as those in the submucous connective tissue of the gullet. Wide distribution of the larvæ within the abdominal cavity has been noted in the case of the experimental animals infested at one definite period, indicating that there is a general scattering of the larvæ of the same age. On account of the interesting distribution of the larvæ observed in experimental calf No. 22 the location of the larvæ will be briefly summarized. This animal had about 300 eggs deposited upon it by flies on March 22 and 28. Most of these were laid in the region of the dewclaws on the hind legs. On July 3 the animal was killed and carefully dissected. In the connective tissue beneath the mucous lining of the gullet 17 larvæ were found. One of these was crushed and its position not noted. The position of these larvæ in the gullet and direction they were headed are shown in Figure 24. Their size ranged from 3.6 to 6 millimeters in length, the average being 5.3 millimeters. On the paunch 12 larvæ were found. Six of these were almost immediately under the spleen, but none were attached to that organ when it was peeled off. The other six were scattered over the rumen at widely varying distances from the gullet entrance. These ranged in size from 5.8 to 8 millimeters, with an average of 6.8 millimeters. Some of these had the anterior end pointing toward the gullet entrance, others were pointing directly away from it, and others were

pointing in various directions. Some of those closest to the gullet entrance were headed toward it. A number were along the line of attachment of the first and second stomachs. On the surface of the second stomach a single larva, 7 millimeters long, was found. On the surface of the colon, about 15 inches from the anus, one larva, 7 millimeters long, was taken headed forward. Seven larvæ were taken in various places in the mesentery of the small intestines. Six of these were 7 millimeters and the other 6.8 millimeters long. One larva, 6.1 millimeters long, was found on the surface of the sixth rib, just under the pleura, about half way between the sternum and the vertebra. This larva was headed ventrally and was rather slender. One larva, 6 millimeters long, was found free on the basal portion of the twelfth rib after the muscular tissue had been stripped off. A careful examination of the other internal organs, diaphragm, muscular tissues of the back, and muscles of the legs was made without finding any indication of the presence of larvæ.

It is noteworthy that the larvæ in the gullet averaged smaller than those in the paunch or elsewhere in the abdomen. This of itself might suggest that the older larvæ were passing backward from the gullet to the paunch or elsewhere. When consideration is given to the fact that larvæ much larger than these are found in considerable

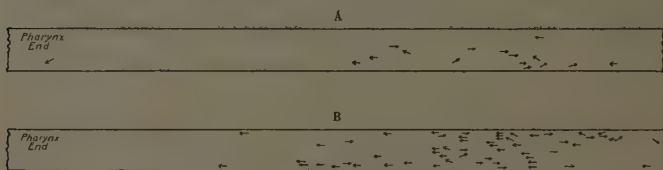


FIG. 25.—*Hypoderma lineatum*: Diagram showing position and direction of travel of larvæ in gullet of calf (No. 409): A, pleural side; B, mucous side

numbers in the gullet during the latter part of summer and throughout the fall, however, the drawing of such a conclusion is hardly justified.

Another experimental calf (No. 409, fig. 25) which was infested with about 268 eggs on the abdomen and hind legs on March 10 and 16 was slaughtered on July 9. A cursory examination of the viscera, walls of the diaphragm, chest, and abdominal cavities failed to reveal any larvæ. On the gullet, however, in the submucous tissue 60 larvæ were found and on the muscle side of the gullet 16 larvæ were taken in the stroma beneath the pleura. These larvæ ranged in length from 5 to 5.6 millimeters, but only a few were carefully measured. The length of those on the pleural side of the gullet was practically the same as those on the mucous side. Of those in the submucous tissue 17 were pointing toward the stomach, 40 toward the pharynx, and 2 were not noted. On the pleural side 9 were pointed toward the stomach and 7 toward the pharynx. The diagram (fig. 25) shows the distribution and the direction of pointing of these larvæ.

The exact course followed by the larvæ in passing from the body cavities to the back has not been determined with accuracy, though the presence of larvæ followed by greenish and gelatinous streaks indicates the lines of migration and the probable routes. The find-

ing of larvæ along the ribs, on the diaphragm, and in the neural canal indicates that they pass from the gullet across the diaphragm to the ventral ends of the ribs and thence follow the connective tissue beneath the pleura up to the back. Some probably work their way between the muscles and pass directly up the diaphragm from the gullet to the back. A number of these no doubt gain entrance to the neural canal, later pass out through the posterior foramen, and then go up to the connective tissue beneath the skin along the back. Both of these routes are probably followed in migrating from the gullet to the back.

The writers' observations indicate that the migration from the gullet to the back is rather rapid. The first larvæ begin to appear in the subdermal tissues of the back very soon after the maximum size has been reached in the gullet. As soon as the number of larvæ are observed to decrease in the gullet they are observed to appear on the back, with practically no increased growth.

Unfortunately it has not been possible carefully to dissect animals infested only with *H. bovis* so as to determine just where the larvæ occur from the time they enter the host until they appear on the back. In New York, where both species are present, the neural canals of 140 slaughtered animals were examined and all the larvæ found were *H. bovis*. Thirty specimens were located, with a maximum of four in one canal. Larvæ were found in this situation during the months of October to March inclusive. The size ranged from 6.5 to 14 millimeters, the larger ones being found later in the season.

At Dallas, Tex., where *H. lineatum* only occurs, about 75 beesves were examined rather carefully as they were dressed. Only one Hypoderma larva was found in the neural canal, a third-stage specimen located in the central portion of the second lumbar vertebra and measuring 14 millimeters in length.

This observation indicates that the larvæ of *H. bovis* enter the neural canals of cattle more frequently than do those of *H. lineatum*. It seems unlikely, also, that all larvæ found in this situation are en route directly to the back, as the larvæ found during October were only from 6.5 to 9 millimeters long, and never have such small larvæ been encountered in the subdermal tissues of the back. Furthermore, the larvæ did not begin to appear under the skin of the backs of cattle in that locality for over three months after these larvæ were taken in the neural canals.

PREPARATION FOR THE EGRESS OF FULLY DEVELOPED LARVÆ

The appearance of third-stage larvæ under the skin on the back is frequently accompanied by considerable local inflammation, indicated by edema of the connective tissue and sometimes marked swellings and soreness.

Certain cattle are more prone to such manifestations and show swellings as large as 10 inches in diameter around each larva as it comes to the subcutaneous tissue of the back. From one to three days after the appearance of one of these swellings a minute hole is cut by the larva near the center, after which the swelling soon subsides. Although no conclusive evidence is at hand, the writers are of the opinion that the holes are cut through the skin almost

immediately after the larvæ reach it, and never more than three days later. Usually the first indication of a break in the skin is in the nature of a minute, irregular hole which is usually accompanied by slight bleeding. Within a day or two after the first break is made the edges of the hole become more smooth and round. In several instances the writers have observed a circular plug of skin about 2 millimeters in diameter and bearing hair, seated in a freshly cut hole. In two cases these plugs were still attached at one side as though the cutting process was not complete.

The only evidence to indicate which end of the larva does the cutting is that in every case where larvæ have been extracted the posterior end is always outward. This has been found even before the cutting of the hole was completed. It is conceivable that the larvæ may do the major part of the cutting with the mouth parts and then turn around and complete the enlarging of the hole with the posterior end. When these early stages are removed by pressure they appear to be in a position perpendicular to the skin rather than lying horizontally under it as is the normal position in subsequent stages.

DEVELOPMENT OF THIRD-STAGE LARVÆ

The first molt under the skin, from the third to the fourth stage, takes place soon after the hole is completed. The determination of this period with exactness is very difficult, but the records of the writers show that the molt in *H. lineatum* may take place in about 24 hours after the hole is completed, or the stage may last from 6 to 8 days. The average period, based on 17 records made at Dallas, Tex., with considerable exactness, is 4.5 days, and the average period based on 13 records made in New York is 4.26 days. The period from the cutting of the hole in the skin to the molt in *H. bovis*, as observed in New York, ranged from 1 to 6 days with an average of 3.35 days.

For several hours prior to the molt the spiracles of the fourth stage can be seen beneath the skin of the larvæ. The exuvia are very delicate, but seem to be shed almost in their entirety at one time. The break in the larval skin is very irregular. The posterior ends of the tracheal tube where they join the spiracles are rather highly chitinized and they are shed along with the skin.

The writers' observations show that not infrequently the third-stage larva may move to a new location under the skin, usually within a few inches of the first, and cut a second hole or even a third hole before it molts.

ENCYSTMENT AND DEVELOPMENT OF FOURTH-STAGE LARVÆ

It appears that about simultaneously with the molt to the fourth stage the tissues of the host change their form of resistance from an active leucocytosis to a segregation of the insects by the formation of encystment sacs (fig. 26). With the development of these pouches the general inflammation of the connective tissue subsides. The skin of the third stage remains in the sac, which is formed very rapidly, and gradually the walls of the sac become thicker as the growth of the larva continues. During this and all subsequent stages the larva remains with its posterior spiracles toward

the hole in the skin, usually keeping them just a short distance below the surface. During the course of development of the fourth stage the hole may be completely closed by scabs, but an effort is always made to keep it open. This frequently results in the formation of what the writers have called "a perforated plug." This apparently consists of secretions which harden within the hole, becoming somewhat free from its edges, and the larva maintains a minute hole through the center of the mass.

During the development of the fourth stage the body is nearly horizontal, the dorsal side outward, and the posterior end bent upward so that the spiracles are close to the aperture in the skin.

The duration of the fourth stage of *H. lineatum* at Dallas, Tex., has been observed in one instance to be from 5 to slightly more than 13 days, and in another from 10 to 13 days. It is thought, however, that the minimum periods mentioned are possibly erroneous, owing to the chance of failure to record the molt to the fourth stage with accuracy, and that 15 days is nearer a true minimum for this stage. The maximum period recorded in one instance was between 44 and 53 days. The average duration of this stage based upon 21 individuals as recorded at Dallas was 24.5 days. The duration of this stage in the backs of cattle in New York is practically the same as in Texas. Some of the records for this stage are given in Table 7.

In *H. bovis* the length of the fourth stage was observed with fair accuracy in 18 specimens in New York. The minimum period among these was 21+ days, the maximum period 35 to 38 days, and the average 27.1 days (see Table 5).

TABLE 5.—Duration of fourth stage of *Hypoderma bovis* in New York

Locality	Larvæ molted to fourth stage	Larvæ molted to fifth stage	Duration of fourth stage
	1921	1921	Days
Herkimer.....	May 10 (before).....	June 1.....	22+
Do.....	do.....	June 7.....	28+
Do.....	do.....	June 9.....	30+
Do.....	May 15 (before).....	do.....	25+
Do.....	May 17.....	do.....	23
Do.....	May 19 (before).....	do.....	21+
Do.....	May 24 (before).....	June 17.....	24+
Do.....	May 25 (before).....	June 18.....	24+
Do.....	do.....	June 20.....	26+
Do.....	May 29.....	June 27.....	29
Do.....	June 2 (before).....	June 25.....	23+
Do.....	do.....	July 3.....	31+
Do.....	June 6 (before).....	July 11.....	35+
	1922	1922	
Middletown.....	Apr. 1 to 3.....	May 8 to 9.....	35 to 38
Do.....	Apr. 8 to 9.....	May 5 to 6.....	26 to 28
Do.....	Apr. 15 to 17.....	May 15 to 16.....	28 to 31
Do.....	Apr. 19 to 20.....	May 14 to 15.....	24 to 26
Do.....	Apr. 22 to 24.....	May 20 to 24.....	26 to 32

The molting of the fourth instar is apparently preceded by a short period of comparative inactivity. The fifth-stage spiracles appear as pale yellow objects deep beneath the integument two or three days before the molt takes place. As the time for molting approaches the spiracles become more distinct in outline and just

prior to the molt their details of structure are well defined beneath the skin of the fourth stage (fig. 6, *g*). As in the preceding molt, the rupture in the integument seems to be irregular and does not

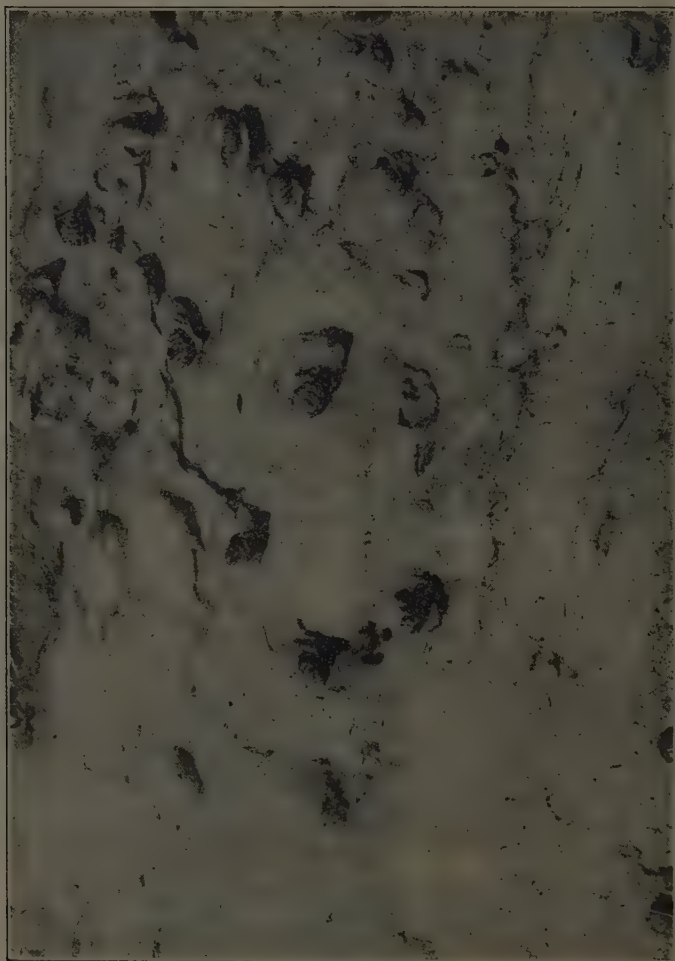


FIG. 26.—Under side of hide just removed, showing cysts, some of which are cut open to expose cattle grubs

always occur in the same place. The exuvium remains in the cysts and can often be removed by continued pressure after the fifth-stage grub has been forced out.

DURATION AND DEVELOPMENT OF THE FIFTH STAGE

Immediately after molting, the larvæ are more or less translucent and the integument comparatively tender. The spiracles at first appear more or less iridescent and are yellowish with a slight orange tinge. Growth in this stage is rapid. The integument becomes heavier and tougher and the spiracles darker. This darkening begins on the rims and gradually the entire spiracles become dark brown to almost black. Along with the darkening of the spiracles and the rapid growth of the larvæ, there is a general darkening of the entire integument. Just prior to emergence from the host the grub becomes shorter and broader. Along with this change comes the darkening of the integument to a deep brown or black.

The duration of the fifth stage is extremely variable. At Dallas, Tex., the minimum length of this stage in *H. lineatum* has been observed to be between 18 and 21 days. More than 100 larvæ were observed. In another instance there was a period of from 19 to 21 days, but it appears that very few complete this stage in less than 23 days. The average, based on 71 records made at Dallas, Tex., was 30.3 days. Some of these records are given in Table 7.

The length of the fifth stage was recorded in six larvæ of *H. lineatum* at Herkimer, N. Y. The maximum was 47 days, the minimum 29 days, and the average 38.5 days. In 1922 in Orange County, N. Y., the length of the instar was determined in 19 larvæ. The maximum was 39, the minimum 16, and the average 29.5 days.

The duration of the fifth stage of *H. bovis* was determined in the case of 58 larvæ at Herkimer, N. Y., in 1921, and in the case of 19 larvæ at Middletown, N. Y., in 1922. The maximum, minimum, and average in the former were 62, 26, and 39.6 days, and in the latter 45, 35, and 40.1 days. Some of these records are presented in Table 6.

TABLE 6.—Duration of fifth stage of *Hypoderma bovis* in New York

Locality	Larvæ molted to fifth stage	Mature larvæ emerged from host	Duration of fifth stage	Locality	Larvæ molted to fifth stage between dates	Mature larvæ emerged from host between dates	Duration of fifth stage
	1921	1921	Days		1922	1922	Days
Herkimer	May 13	June 27	45	Middletown	Apr. 1 and 3	May 11 and 13	38 to 42
Do.	May 18	June 30	33	do.	Apr. 10 and 13	May 20 and 24	37 to 44
Do.	do.	June 18	31	do.	Apr. 19 and 20	June 1 and 3	42 to 45
Do.	May 19	do.	30	do.	Apr. 24 and 22	June 3 and 5	42 to 45
Do.	do.	June 14	26	do.	Apr. 22 and 24	May 31 and June 3	37 to 42
Do.	do.	June 28	40	do.	do.	June 1 and 3	38 to 42
Do.	May 21	July 4	44	do.	Apr. 25 and 26	June 7 and 9	42 to 45
Do.	May 25	June 20	26	do.	Apr. 26 and 27	June 5 and 7	39 to 42
Do.	May 27	July 4	38	do.	do.	June 7 and 9	41 to 44
Do.	May 31	July 7	37	do.	Apr. 26 and 28	do.	40 to 44
Do.	June 2	July 14	42	do.	do.	do.	40 to 44
Do.	June 4	July 16	42	do.	Apr. 27 and 28	June 3 and 5	36 to 39
Do.	June 6	Aug. 7	62	do.	do.	do.	36 to 39
Do.	June 9	July 17	38	do.	Apr. 29 and May 1	June 5 and 7	35 to 39
Do.	June 10	July 20	40	do.	May 1 and 2	June 7 and 9	36 to 39
Do.	do.	July 25	45	do.	May 4 and 5	June 12 and 14	38 to 41
Do.	June 27	Aug. 4	38	do.	May 5 and 6	June 14 and 16	39 to 42
Do.	June 29	Aug. 9	41	do.	May 12 and 13	June 19 and 21	37 to 40

It is in this fifth or last larval stage that stockmen usually observe the presence of the grubs, as the sizes of the lumps increase with the growth of the larvæ. The sizes of the openings through the skin

vary considerably, but they are usually much larger after the molt to the fifth stage, and measure from 3 to 4.5 millimeters in diameter (fig. 27). It is seldom that any scabbing or other obstruction is found in the aperture over a fifth-stage larva. There is usually to



FIG. 27.—Close view of portion of cow's back infested with cattle grubs. Hair is clipped from around holes

be seen a rim of exudate, part of which is considered to be excrement, around the outside edge of each hole.

The position of the larva is similar to that in the fourth stage. The posterior end of the segments is bent slightly so as to bring the

spiracle to the hole and almost perpendicular to it. Thus the hole in the skin is always near the posterior end of the larva, which may have the anterior portion in any direction. The majority of the cysts have the aperture near the upper side.

TOTAL DEVELOPMENTAL PERIOD IN THE BACKS OF CATTLE

As with other stages of *Hypoderma*, there is a variation in the total period required for the development of the larvæ from the time the holes are cut through until the larval growth is completed. The determination of this period with accuracy is of much importance in control and especially in eradication work, since the interval between treatments should be governed by such data.

In a large number of cattle of several breeds warbles of both species were followed through their entire development in the subdermal tissue. Owing to the high mortality among the larvæ, especially when examined repeatedly to determine molts, etc., only a comparatively few records of complete development were obtained among the hundreds of warbles observed.

In order that the duration of the larval stages might be determined various individual cattle were observed from

the time warbles began to appear until all grubs had made a normal egress. These observations were made as frequently as time would permit, usually once each day. Through practice the touch was developed to a high degree and one could readily detect the first indication of a foreign object under the skin or a minute amount of exudate from a puncture of the skin.

In making the examinations a headlight was developed which proved of great value (fig. 28). It consisted of a shortened flash light attached to a head band, and served by two dry cells carried on a belt. The focus was adjusted to permit the observer to use a hand lens.

With the younger stages of the larvæ in particular it was found necessary to apply pressure around them to force them toward the



FIG. 28.—Headlight outfit used in examining cattle grubs in cysts

surface, where they could be seen distinctly. Not only the time of molting was observed in this way but the changes in color of the last stage could be observed and the approach of complete development noted and emergence watched for.

In order to eliminate any possible adverse effect on the development of the larvæ by these repeated observations, the appearance in the subdermal tissues of several hundred third-stage larvæ was determined by the method indicated, following which they were not disturbed except to make occasional notes on their presence until about the date of emergence from the host. The average time for the development in the case of those larvæ examined for molts, etc., was practically the same, however, as in the case of those which were not disturbed.

As a method of checking up on the observations on the various larvæ it was found best to make a rough diagram of the backs of the hosts, indicating the position of each larva and assigning it a number. In order to facilitate the location of each larva the position on the animal's back was indicated by clipping the hair. In the early observations the hair was clipped close to the skin immediately over the warble hole. Later, as it was thought that the development might be interfered with by exposure, clips were made in the hair of the host just above or below the position of the warble.

The minimum period of development of larvæ of *H. lineatum* in the backs of cattle at Dallas, Tex., based on about 200 records, was between 35 and 47 days. Another period noted was 38 to 40 days, and still another 39 to 46 days. In several other cases the period ranged between 39 and 50 days. The maximum period was between 78 and 89 days. The average total developmental period, based on 104 warbles examined at frequent intervals, was 56.3 days. A few representative records of the development in the backs of cattle are given in Table 7.

The average period of development of 222 other larvæ of *H. lineatum* in which the date of appearance under the hide and the date of emergence from the host were determined without disturbing the larvæ by making observations on molts was 57.74 days.

At Uvalde, Tex., D. C. Parman recorded the duration of the larval period in the backs of cattle for larvæ of *H. lineatum*. The minimum period noted was 43 to 45 days, the maximum 54 days, and the average 49.4 days.

Six accurate records of the period of development of *H. bovis* in the backs of cows were made in New York. The maximum was 77 days, the minimum 65 days, and the average 72.8 days.

Apparently the duration of development in the backs of cattle is not influenced by individual, breed, or age of the host. The writers' records indicate that the development may be slightly shorter at Uvalde, Tex., than at Dallas, and that the time spent in the subdermal tissues of cattle averages slightly longer in the case of larvæ coming up to the backs in the early part of the season. For example, the average period of those which appeared in the subdermal tissue in October and early November was about 58 days, whereas in those which appeared during the latter part of December and in January it was about 51 days.

TABLE 7.—*Development of Hypoderma lineatum in backs of cattle, Dallas, Tex.*

Larvæ appeared between dates	Larvæ molted to fourth stage between dates	Duration of third stage ¹	Larvæ molted to fifth stage between dates	Duration of fourth stage ¹	Duration of third and fourth stages ¹	Emerged from host between dates	Duration of fifth stage	Total period in back of host ²
1919-20	1919-20	Days	1919-20	Days	Days	1920	Days	Days
Oct. 27 and Nov. 3	Dec. 11 (before)	3 to 4	Dec. 20 and 22	47 to 56	47 to 56	Jan. 20 and 24	29 to 35	78 to 89
Nov. 12 and 19	Dec. 12 (before)	3 to 4	Dec. 23 and 25	35 to 44	35 to 44	Jan. 24 and 28	29 to 35	66 to 77
Nov. 19	Dec. 13 (before)	8 to 11	Dec. 15	26	26	Jan. 14	30	56
Nov. 19 and 26	Dec. 13 (before)	8 to 11	Dec. 17 and 18	21 to 29	21 to 29	Jan. 12 and 16	25 to 30	47 to 53
Nov. 20 and 28	Dec. 12 (before)	3 to 4	Dec. 18 and 16	17 to 27	17 to 27	do.	27 to 34	47 to 53
Dec. 1 and 2	Dec. 6 (before)	3 to 4	Dec. 12 and 15	14 to 25	14 to 25	Jan. 6 and 8	22 to 27	39 to 49
Dec. 2 and 3	Dec. 13 (before)	3 to 4	Dec. 22 and 24	20 to 23	20 to 23	Jan. 20 and 24	27 to 33	49 to 54
Dec. 3 and 4	Dec. 13 (before)	3 to 4	Jan. 3 and 8	29 to 37	29 to 37	Jan. 26	26 to 35	54 to 55
Dec. 4 and 5	Dec. 9	8 to 10	Dec. 27	+15	+15	Feb. 3 and 7	26 to 35	60 to 67
Dec. 4 and 5	Dec. 13 (before)	8 to 10	Dec. 23 and 26	10 to 13	10 to 13	Jan. 24 and 28	25 to 32	51 to 56
Dec. 5	Dec. 8 (before)	4 to 5	Dec. 24 and 26	15 to 17	15 to 17	Jan. 20 and 24	25 to 32	46 to 52
Dec. 5	Dec. 17 (before)	3 to 4	Dec. 22 and 23	14 to 15	17 to 19	Jan. 24 and 28	29 to 35	50 to 55
Dec. 5	Dec. 11	3 to 5	Dec. 31 and Jan. 2	+14 to 16	26 to 28	Jan. 20	28 to 29	46 to 47
Dec. 6 and 8	Dec. 9 (before)	4 to 7	Dec. 28 and 29	15 to 18	18 to 23	Jan. 28 and Feb. 3	26 to 34	54 to 60
Dec. 6 and 9	Dec. 13 (before)	4 to 7	Jan. 6	20 to 23	29 to 31	Jan. 24 and 28	26 to 33	47 to 53
Dec. 9 and 11	Dec. 11 and 13	5 to 7	Dec. 29 and 31	20 to 23	20 to 25	Jan. 29	23	52 to 54
Dec. 12 and 15	Dec. 16 (before)	5 to 7	Jan. 8 and 12	26 to 30	30 to 37	Jan. 28 and Feb. 3	28 to 36	50 to 59
Dec. 12 and 16	Dec. 20	5 to 8	Jan. 18 and 26	+5 to 13	9 to 20	Feb. 7 and 11	26 to 34	60 to 67
Dec. 24 and 26	Dec. 26 and 29	0 to 5	Jan. 3 and 6	21 to 28	23 to 28	Jan. 20 and 24	23 to 37	42 to 49
Dec. 31 and Jan. 2	Jan. 2 and 6	0 to 6	Dec. 31 and Jan. 6	11 to 17	13 to 17	Feb. 7 and 11	22 to 39	38 to 54
			Dec. 22 and 26	22 to 25	16 to 25	Jan. 24 and 28	22 to 35	44 to 50
			Jan. 20	14 to 22	25 to 27	Jan. 28 and Feb. 3	22 to 34	44 to 53
			Jan. 20 and 24	14 to 22	25 to 27	Jan. 24 and 28	29 to 37	39 to 47
						Feb. 20 and 24	31 to 39	56 to 66
							27 to 35	49 to 55

¹ Duration of stages includes shortest and longest possible periods.² Figured from date larvæ appeared to date of dropping from the host and not from addition of days in each stage, as it was impossible to get accurate records on the duration of larval stages.

THE METHOD OF EGRESS OF GRUBS FROM BACKS OF CATTLE

When the fifth-stage larvæ complete their growth they become more active and the posterior segments are extended and forced into the openings through the skin and then quickly withdrawn. With this action the sides of the holes are cleaned of the rim of exudate and more or less covered with the pus forced up by the larvæ. When the actual process of emergence begins the posterior segments are forced into the aperture and the larvæ slowly work their way out by expansion and contraction of the body rings. The actual process of emergence of the grubs takes from one to

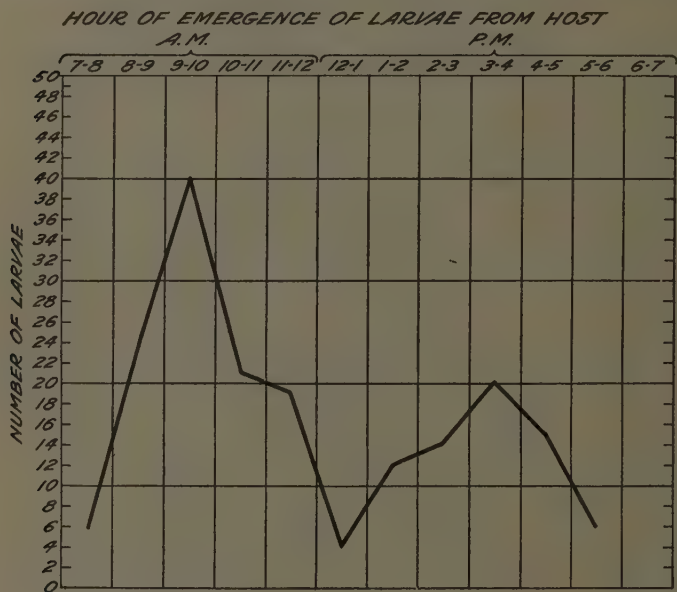


FIG. 29.—Diagram showing hours when larvæ of *Hypoderma lineatum* emerge from the host for pupation

three minutes, but the preparatory activities may be begun several hours before the grubs make a serious attempt to escape.

TIME OF EMERGING FROM HOST

With *H. lineatum* fairly accurate observations have been made on the time of day when 181 warbles emerged from the host, and less accurate observations on 211 others. Glaser (29) pointed out that he observed in Germany a large percentage of warbles dropped in the early morning hours, the percentage being from 49.4 to 68.2 between the hours of 5 and 7 a. m. The writers' observations do not agree closely with his in this respect, for, as is shown on the accompanying diagram (fig. 29), the largest number dropped in the middle of the forenoon from 8 to 10 a. m., and the emergence

was greatly reduced in the middle of the day, increasing again in the middle of the afternoon.

The number of larvæ recorded as dropping in the earlier morning hours is undoubtedly too small, as fewer examinations were made between 8 and 9 a. m. than in later periods, and a much smaller number still between 7 and 8 a. m. It is believed, however, that by adding all of those which may have dropped between 7 and 9 a. m. the total would not nearly equal the number which dropped between 9 and 10 a. m. Of the 269 larvæ the hour of emergence of which was noted with considerable accuracy, 140, or 52 per cent, left the host between 8 a. m. and noon, and 129, or 48 per cent, between noon and 6 p. m. There is undoubtedly a greater disparity than these percentages indicate, as the number of hours in the forenoon period was smaller than the number in the afternoon. Also, as stated above, some warbles that dropped in the early morning hours were not recorded.

The percentage of grubs dropping in the night was comparatively small. Considering the entire 392 larvæ upon which the writers have records, only 88, or 22.4 per cent, dropped out during the 12 hours from 6 p. m. to 7 a. m. As a matter of fact, this percentage is too high, as in it are included larvæ which on several occasions were found to have dropped from animals when they were first examined in the morning; sometimes this examination being made as late as 8 or 9 o'clock.

From their observations and the study of the data accumulated the writers are led to believe that the activity of the host has much to do with the dropping of the larvæ. Feeding of the animals usually took place between 8 and 9 a. m. and up to about that time the animals were comparatively quiet, usually lying down. In the noon period following the morning feeding they again became quiet and lay down much of the time, until 4 or 5 p. m., when feeding again took place. Just how activity of the host should influence the dropping of the larvæ it is not easy to see. Possibly the muscular movements stimulate them. There is a possibility also that the warming up of the back of the animals by the sun following the cool night may tend to stimulate dropping. In the instances cited by Glaser it appears that feeding took place very early in the morning and hence his observations may tend to substantiate this hypothesis.

DISTRIBUTION OF THE LARVÆ ON THE BACKS OF CATTLE

As is well known, the larvæ occur in the greatest numbers along each side of the spinous processes from the shoulder to the hip bones. In diagramming the backs of hundreds of cattle the writers have observed that this distribution is very irregular, sometimes several larvæ being in one group and the rest of the back comparatively free, while in other cases they are widely scattered over the entire area. It seems certain, however, that this is simply a matter of chance. In summarizing their figures on the distribution of the larvæ the writers find that about 50 per cent of them occur in the region of the dorsal vertebrae and the other 50 per cent in the lumbar region. As a rule they are more concentrated in the area over the last three ribs. Although it is not unusual to find grubs on

the shoulders, that is, above the scapulas or behind the hip bones, the percentage occurring in these regions is comparatively small, the writers figures indicating slightly less than 1 per cent for the latter. Occasionally grubs are met with on the tail 3 or 4 inches below its base, and also on the neck some inches in front of the shoulders. One instance of the occurrence of a grub below the point of the pin bone has been observed by the writers. Laterally most of the grubs are confined to a strip about 1 foot on each side of the backbone in grown animals, but it is not especially unusual to find them on the ribs half way down the side of the animal. The midline of the back is comparatively free (fig. 30).

The writers' experiments show that there is no relation between the distribution of the eggs on the host and that of the late stages



FIG. 30. -Cow with back infested with cattle grubs. Hair is clipped from around holes

of the larvæ resulting therefrom. As the larvæ are known to migrate freely all through the host, such a relationship would not be expected.

PUPATION AND DURATION OF THE PUPAL STAGE OF *HYPODERMA LINEATUM*

When the larvæ have freed themselves from the hole in the skin in the back of the host they begin contracting and expanding and soon roll off on the ground. For the collection of larvæ as they emerged from the hosts, burlap bands were placed around the bodies of cattle, as shown in Figure 31. They are not very active and their progress in crawling is very slow. There is a tendency for the larvæ to crawl under any loose objects which may be at hand and which would offer some protection; but ordinarily they do not go more than a short distance from the place where they drop, and their

tendency to dig into the ground is not very marked. Not infrequently specimens will bury themselves in loose debris, such as straw and broken leaves, but they do not burrow into compact soil or sand to any extent. The larvæ show marked negative heliotropism, and one was observed to crawl more than 10 feet, seeking shade in which to pupate. Usually within a few hours they become quiet and within 1 to 12 days the integument hardens and changes its shape into the typical puparium form. The average prepupal period recorded in the case of 238 larvæ of *H. lineatum* was 3.4 days. Representative records are presented in Table 8. The prepupal stage observed among 7 specimens, kept in a screened insectary in Middletown, N. Y., in 1922, ranged from 1 to 4 days. This period may vary several days in the case of larvæ leaving the host the same day, but the total time required for their transformation to adult is not increased to that extent.

It is evident that where the larvæ drop normally the prepupal period is markedly influenced by temperatures.

The pupal period at Dallas, Tex., ranged from 16 to 75 days, the average being 38.2 days, as recorded for 196 specimens. Representative data are given in Table 8.

TABLE 8.—Duration of prepupal and pupal stages of *Hypoderma lineatum* at Dallas, Tex.

Larvæ emerged from host		Pupated		Pre-pupal period	Flies emerged			Pupal period	Period from dropping to adult	Temperature dropping to adult		
Date	Number	Date	Number		Date	Number of males	Number of females			Max.	Min.	Average daily mean
1916												
Feb. 17	1	Feb. 21	1	3½	Mar. 21	1	1	+29	33	91.5	23.7	58.26
Feb. 18	1	do.	1	3	Mar. 20	1	1	28	31	91.5	23.7	57.71
Feb. 21	1	Feb. 22	1	¾	Mar. 21	1	1	+28	29	91.5	23.7	58.94
Do.	1	Feb. 23	1	2	Mar. 22	1	1	28	30	97.9	23.7	59.68
Feb. 22	3	Feb. 24	3	2	do.	2	1	27	29	97.9	23.7	59.80
Mar. 4	1	Mar. 6	1	2	do.	1	1	16	18	97.9	28.0	64.65
Mar. 6	1	Mar. 7	1	1	Mar. 23	1	1	21	22	97.9	34.0	64.32
Mar. 7	1	Mar. 8	1	1	do.	1	1	20	21	97.9	34.0	63.77
1917												
Jan. 31	1	Feb. 3	1	3	Mar. 13	1	1	38	41	93.0	9.5	50.92
Feb. 13	2	Feb. 17	2	4	Mar. 20	1	1	31	35	93.0	25.0	56.22
Mar. 10	1	Mar. 11	1	1	Mar. 31	1	1	20	21	87.5	32.0	63.31
1918												
Jan. 20	2	Jan. 25	2	5	Mar. 11	2	1	45	50	97.5	33.5	49.46
Jan. 31	2	Feb. 6	2	6	Mar. 13	1	1	35	41	97.5	12.5	53.86
1920												
Jan. 6	1	Jan. 8	1	2	Mar. 18	1	1	70	72	81.0	19.0	48.67
Jan. 7	1	Jan. 18	1	11	do.	1	1	60	71	81.0	19.0	48.83
Jan. 9	1	Jan. 16	1	7	Mar. 25	1	1	69	76	81.0	19.0	51.31
Feb. 6	1	Feb. 9	1	3	do.	1	1	45	48	81.0	19.0	52.46
Feb. 18	1	Feb. 20	1	2	Mar. 27	1	1	36	38	81.0	19.0	54.08
Feb. 23	1	Mar. 1	1	7	Mar. 25	1	1	24	31	81.0	19.0	52.61
1921												
Jan. 11	1	Jan. 15	1	4	Mar. 1	1	1	45	49	83.0	26.0	52.03
Do.	1	Jan. 17	1	6	Mar. 3	1	1	45	51	83.0	26.0	52.44
Jan. 28	1	Jan. 29	1	1	Mar. 12	1	1	42	43	83.0	27.0	54.91
Feb. 5	2	Feb. 7	2	2	Mar. 15	1	1	36	38	83.0	28.0	56.89
Feb. 6	1	Feb. 8	1	2	do.	1	1	35	37	83.0	28.0	56.94
Do.	1	Feb. 10	1	4	do.	1	1	33	37	83.0	28.0	56.94
Feb. 13	2	Feb. 14	2	1	Mar. 16	1	1	30	31	83.0	28.0	58.90

Only four adults of *H. lineatum* were bred out in Middletown, N. Y. Among these the pupal period ranged from 26 to 41 days, and the period from date of leaving the host to emergence of the adult ranged from 27 to 42 days. At Dallas, Tex., this period of transformation ranged between 18 and 77 days, with an average of 41.7 days in the case of 221 specimens kept out of doors.

The average period of transformation was slightly shorter in males than in females, being 42 days in the former and 44.4 in the latter, as computed on 92 males and 80 females.

Hadwen (33) has presented records of the duration of the pupal stage of *H. lineatum* of from 13 to 19 days when the specimens were kept in an incubator at 32° C., and Glaser (30) records a pupal period in Germany for this species of 23 to 38 days. Carpenter (12, 17) states that he has observed the pupal period to be about 7 to 8 weeks in Ireland.



FIG. 31.—Heifer with bagging around body, for purpose of collecting cattle grubs as they emerge from host

PREPUPAL AND PUPAL STAGES OF *HYPODERMA BOVIS*

Mature larvæ of *H. bovis* show about the same degree of activity after emergence from the host as those of *H. lineatum*, but they seem to have a stronger tendency to burrow into the soil. The larvæ of this species also show a great de-

sire to escape from direct sunlight, and one was observed to crawl 12 feet to a deep shadow, where it pupated. If placed on loose soil, most of them will bury themselves in a short time. Some burrow down about an inch, but most of them go just below the surface.

When the weather is warm the prepupal period is very short. At Dallas records were kept on several larvæ which emerged normally from cattle. All of these pupated, and 4 produced adults. The prepupal period of these larvæ was in every case somewhat less than a day, and the pupal period of the 4 which emerged was from 14 to 15 days, making a total period from emergence from the host to the appearance of the adult insects of from 15 to 16 days. Among 24 larvæ extracted from cattle at Dallas, Tex., and kept for rearing, 14, or 58.3 per cent, pupated and only 1 (4.2 per cent) produced an adult. In the case of this specimen the prepupal period was slightly more than a day, and the pupal period 14 days, a total transformation period of 15 days. The writers succeeded in breeding out 4 adults from 8 mature larvæ extracted from cattle at Herkimer, N. Y. (Table 9). The prepupal period among these was 10 hours to 1 day, and the pupal period from 15 to 24 days. The total developmental period from extraction of the larvæ to the

emergence of the adults was 16 to 25 days. All of these records were made in midsummer, and the specimens reared in New York were kept in a building in which the temperature was warmer than outdoors, hence the periods shown are probably shorter than would occur normally.

TABLE 9.—Duration of prepupal and pupal stages of *Hypoderma bovis*

Locality	Date dropped or extracted from host	Date pupated	Duration of pre-pupal stage	Adults emerged			Duration of pupal stage	Period from dropping to adult	Temperature during period from dropping to adult		
				Date	Number of males	Number of females			Max.	Min.	Average daily mean
Dallas, Tex.	1918 May 15	1918 May 16	Days 1	1918 May 30		1	Days 14	Days 15	° F. 98.4	° F. 54.0	° F. 78.28
Do.	May 24	May 25	1	June 8	1	1	14	15	96.0	63.1	81.62
Do.	May 27	May 28	1	June 12		1	15	16	97.0	65.0	81.37
Herkimer, N. Y.	1921 June 24	1921 June 24		1921 July 11		1	16½	+17			
Do.	July 14	July 15	1	July 30		1	15	16			
Do.	July 17	July 17	½	Aug. 5		1	18½	+19			
Do.	Aug. 3	Aug. 4	1	Aug. 28	1		24	25			
Middletown, N. Y.	1922 Apr. 20	1922 Apr. 27	7	1922 June 4	1		38	45	85.0	28.0	58.
Do.	Apr. 21	do.	6	do.	1	1	38	44	85.0	28.0	59.1
Do.	Apr. 23	do.	4	do.	1	1	38	42	85.0	32.0	60.0
Do.	Apr. 26	do.	1	do.	1	3	38	39	85.0	32.0	60.9
Do.	Apr. 28	May 1	3	do.	2	1	34	37	85.0	33.0	61.4
Do.	do.	do.	3	do.	3		34	37	85.0	33.0	61.4
Do.	Apr. 29	do.	2	do.	1	3	34	36	85.0	33.0	61.9
Do.	do.	do.	2	June 5	1	2	35	37	85.0	33.0	62.1
Do.	Apr. 30	do.	1½	June 4	1	1	33½	35	85.0	33.0	62.1
Do.	May 4	May 8	4	June 6	1		29	33	85.0	40.0	62.8
Do.	do.	do.	4	June 7	6		30	34	85.0	40.0	63.2
Do.	do.	do.	4	June 8	1	2	31	35	89.0	40.0	63.6
Do.	May 8	May 9	1½	June 7	5		28½	30	85.0	40.0	63.8
Do.	do.	May 10	2	June 9		2	30	32	91.0	40.0	64.6
Do.	May 12	May 13	1	June 8	3		26	27	89.0	40.0	64.5
Do.	do.	do.	1	June 9	3	4	27	28	91.0	40.0	64.9
Do.	do.	do.	1	June 10	1	1	28	29	92.0	40.0	65.3
Do.	May 14	May 15	1½	June 9	3	1	24½	26	91.0	41.0	65.0
Do.	do.	do.	1½	June 10	1		25½	27	92.0	41.0	65.5
Do.	do.	do.	1½	June 11		1	26½	28	92.0	41.0	65.8
Do.	May 17	May 19	1½	do.	1		23½	25	92.0	41.0	66.5
Do.	do.	do.	1½	June 12		1	24½	26	92.0	41.0	66.8
Do.	May 20	May 21	1	June 11	1		21	22	92.0	41.0	67.8
Do.	do.	do.	1	June 12		1	22	23	92.0	41.0	68.2
Do.	May 25	May 26	1	June 16	2		21	22	92.0	41.0	68.3
Do.	May 27	May 29	2	June 19	1		21	23	92.0	41.0	68.1

¹ Half days are given to approximate more closely the time required for transformation.

At Middletown, N. Y., during 1922, a large number of adults were reared from larvæ which emerged normally from the backs of cattle. These pupæ were kept in a screened, roofed insectary out of doors. The prepupal period ranged from about 10 hours to 7 days, with an average of 1.7 days; the pupal period, from 21 to 38 days with an average of 29.4 days. The time from leaving the host to emergence of adults varied from 22 to 45, with an average based on 167 records of 31.34 days. The longest period (Table 9) occurred in the spring. As some larvæ left hosts in 1922 about April 1, it is probable that some periods longer than the maximum shown might have occurred among the larvæ dropped earlier in the spring.

In Canada, Hadwen (34) observed a period of 30 to 40 days to intervene from the emergence of the larvæ to the appearance of

the adult, the average for several being 34.7 days, and Glaser (29) records this period as being 37 to 56 days in Germany. Under just what conditions these pupæ were kept is not known, but presumably they were out of doors. Vaney (106) in Lyons, France, has observed that the period of transformation requires from 3 to 4 weeks. In the vicinity of Paris, France, Lucet (63) records an average pupal period of 32.9 days, the range being from 29 to 40 days. In Ireland, Carpenter, Phibbs, and Slattery (19) record a pupal period of 32 to 46 days. Stub (97), working in Copenhagen, found the pupal period to be from 40 to 53 days.

MORTALITY IN THE PREPUPAL AND PUPAL STAGES

Among larvæ which drop normally a considerable percentage fail to produce flies, even under what might be thought to be optimum conditions. The percentage of the larvæ which pupate is rather high. Among 559 larvæ of *H. lineatum* which were noted at Dallas, Tex., 514, or 92 per cent, formed pupæ and 337, or 65.6 per cent, of the pupæ emerged as adults, or 60.3 per cent of the total number. Both species of *Hypoderma* are very dependent upon proper conditions for completion of their development. Larvæ removed from the backs of cattle before they are ready to emerge are subject to a high percentage of mortality. It is conceivable that by forcing them through the holes in the hide they may be injured, but the writers' experience indicates that immaturity and not injury is the cause of death. Among 325 well-developed larvæ of *H. lineatum* extracted by hand and kept under optimum conditions for pupation and adult emergence, only 113, or 34.8 per cent, pupated, and out of this number 26, or 23 per cent, produced adults. This was 8 per cent of the total number of the larvæ extracted and observed. All of these larvæ had practically attained their full growth.

Among 221 larvæ of *H. bovis* which emerged normally from hosts and were kept in a screened insectary in Middletown, N. Y., 186, or 84 per cent, produced adults.

Excessive moisture produces a high mortality among pupæ. This point will be discussed under natural control.

EMERGENCE OF ADULT FROM PUPARIUM

In the case of both *H. lineatum* and *H. bovis* the flies appear mature within the puparia several hours before they emerge. The majority of the adults reared by the writers have been found to escape from the puparia during the early morning hours.

The cap of the puparium is first forced open by the head of the fly, and in some cases it is broken off completely. The fly then crawls out, and this process takes less than half a minute. Within a few minutes after the fly escapes it usually walks away from the puparium and begins to unfold its wings. Usually this process requires about five minutes. The ptilinum is completely retracted and the wings straightened to normal position in about 15 minutes after emergence. The abdomen is conspicuously distended, showing that the insect is provided with an ample supply of food from the larval stage. An occasional droplet of excrement is voided during the drying process. Immediately after the wings are dried

the abdomen is extended and retracted and the insect makes clumsy attempts at flight. Within half an hour after emergence it is able to sustain itself on wing, though rather clumsily.

The adults evince a very strong positive heliotropism. In captivity their main energies are devoted toward escaping. Very few flies have been recovered in nature unless in the act of attacking cattle, and just what place they choose for resting is not known. Apparently, however, they remain on the ground or on grass and shrubbery close to the ground.

PROPORTION OF SEXES

The sexes were noted in the case of 284 reared adults of *H. lineatum*. Of these, 147, or 51.8 per cent, were males. The males usually emerge from the puparia slightly before the females, although this is not uniformly the case. Among 172 adults of *H. bovis* which were reared and the sex noted, 81, or 47.1 per cent, were males.

FOOD OF THE ADULT

Mention has been made of the supply of food carried over to the adult stage from the larvæ. This appears to be sufficient to meet the needs of the adult insect throughout its life. The writers have repeatedly attempted to feed reared adults in captivity on fruit, sirup, and water, but have never observed any indication that they would partake of such substances. The mouthparts are degenerate and probably not capable of functioning in feeding.

MATING

Many reared flies of *H. lineatum* have been kept in various types of breeding cages, usually supplied with sticks or branches of green trees, and in the much greater number of these cases mating was not observed to take place. Although a number of these reared females were induced to oviposit, in most instances the eggs were infertile. In four cases mating was closely observed. The act usually took place immediately after the males and females were placed in the same small cage. In each instance the male seized the female as soon as they met, but in one case the male went through some preliminary courting actions. He crawled over the female's back and head, then worked rearward on the back of the female and mating began. The details of mating appear to be about the same as with many other Diptera. The duration of the act ranges from one to three minutes. In two instances mating was repeated a second time immediately after the first. In two of the four instances of mating observed in *H. lineatum* both the male and female were 1 day or more old. In the other instance, however, which occurred at 10.45 a. m., the male had emerged shortly prior to 9. a. m. of the same day, and the female was observed to crawl from the puparium at 10 a. m.; thus mating took place when the female had been out only 45 minutes. It is interesting to note in this connection that this female upon being placed on a calf 20 minutes after mating deposited a considerable number of fertile eggs.

H. bovis evidently mates much more freely in captivity than *H. lineatum*. The act has been observed in many instances to take

place among reared specimens. Among a large number of adults of *H. bovis* which emerged early in the morning and were kept in lantern globes, many pairs were observed in copula about 10 a. m. as the temperature rose. The duration of the act ranged from two to two and one-half minutes.

OVIPOSITION

Reference has been made already to an instance of a fly beginning oviposition within about an hour of the time she emerged. The writers' observations in the field indicate that if favorable weather conditions prevail oviposition usually begins on the same day the adults emerge. It also appears that with flies in the field and with those captured and placed on experimental animals the majority of the eggs deposited by an individual are laid during a single day. In several instances flies deposited a large number of eggs during one day and a moderate number during the second day, but in no case have specimens oviposited during three successive days.



FIG. 32.—Heel fly (*Hypoderma lineatum*) ovipositing upon leg of cow

As has been pointed out by Hadwen and other authors, the methods of oviposition are very different in *H. lineatum* and *H. bovis*. The former attacks more stealthily than the latter, and several eggs are usually placed on a single hair, while with *H. bovis* the eggs are laid singly. This difference in the action

of the flies during their oviposition is intimately associated with the fright produced among cattle, as will be discussed later.

In the field when cattle come in the vicinity of a resting female of *H. lineatum* the insect is observed to approach them on the wing, usually alighting on the ground close to an animal and frequently approaching the hind legs of the host by a series of short flights which resemble jumps. She sometimes lights directly on the heel, usually below the dewclaws, and immediately begins to extend the ovipositor, grasping the hair and cementing on her eggs (fig. 32). In other instances if the animal is not moving she may come close to the heel of the host, turn around, and back up to the rear of the hoof with the ovipositor extended. In this way the short hairs between the hoofs are reached and the eggs are placed in position

while the fly remains on the ground. When the animal moves, the fly usually follows, flying behind close to the ground, and when the opportunity offers she may alight on the host, commonly on the hind legs below the hock. Under such conditions the animal is usually aware of the presence of the fly and often kicks at it, frequently knocking it to the ground, in which case it usually arises promptly and starts again after the host. With animals disturbed in this way the fly is more likely to attack higher on the legs and not infrequently on the sides, especially in the region of the flank or on the forelegs or shoulders.

In many instances the writers have observed females of *H. lineatum* to oviposit on cattle while they were lying down. When not disturbed the fly usually deposits a series of eggs, possibly 50 to 60, in rapid succession and then rests for a minute or two. Sometimes she moves slightly to a new position and then repeats the operation.

Flies of *H. lineatum* captured by means of a net while attacking cattle in nature are readily induced to oviposit on experimental animals kept under control; in fact, this was the method followed in obtaining eggs with which to infest experimental animals and for other purposes. After the flies were captured they were usually placed in small tubes or jars and brought immediately to the laboratory and placed upon experimental hosts. To accomplish this the female was usually placed in a glass vial with the open end placed against the host. Usually as soon as the fly comes in contact with the hair of the animal she begins extending the ovipositor and starts laying eggs. After she has once begun it is often unnecessary to keep the restraining vial over her.

H. bovis attacks the animals viciously, usually approaching them about the height of the hock, and very seldom lights on the ground. On account of its more persistent and ferocious attack the animals are put to flight with the first period of oviposition. The fly strikes the animal a number of times in rapid succession, cementing an egg on a hair in nearly every instance. After a number of these strikes at the animal the fly may leave for a few minutes and then return and repeat the process as persistently as before. Frequently when the host is active the fly may follow it around a small pasture, attacking repeatedly when it catches up to the fleeing animal.

Great difficulty was experienced in getting females of *H. bovis* to deposit eggs after they had been captured. Hawden's reports indicate that he had no difficulty in getting females caught while ovipositing in nature to deposit under an insect net held to a bovine or when released near a tethered animal. In Illinois and New York, however, a number of flies captured in the field by the writers and applied in various ways to hosts under control gave very discouraging results. Only a few eggs were secured and these for the most part were dropped free in the hair.

During the summer of 1922 a large number of flies of both sexes of *H. bovis* were reared at Middletown, N. Y., and many attempts were made to secure eggs from them. Although they mated freely, as has been stated, they persistently refused to oviposit. Some were kept in glass containers held against a calf; others were placed in small screen cages attached to the host; and still others were liberated

in cages containing calves. But in no case were any eggs deposited normally.

On account of the fact that *H. lineatum* deposits its eggs in series on the same hair, the rate of egg laying is somewhat faster than with *H. bovis*. In some instances the eggs of *H. lineatum* have been seen to be deposited at the rate of nearly 2 per second, and 30 or 40 may be deposited in a minute.

NUMBER OF EGGS DEPOSITED

The number of eggs deposited, especially by *H. bovis*, is very difficult to determine. The maximum number observed by the writers for *H. lineatum* was 446. These were deposited by a female taken in the act of ovipositing on a cow in a pasture, and hence this fly may have laid many eggs before capture. Glaser (29) has observed a female *H. lineatum* to deposit 538 eggs, and estimates the total number deposited by this female as 550. In many instances from 200 to 300 eggs have been obtained from a female caught in the field in the act of oviposition. Females dissected after they have become too weak to deposit more eggs usually have a good number of ova left in the abdomen, although many of these appear to be only partially developed.

CONDITIONS UNDER WHICH OVIPOSITION TAKES PLACE

Both species of *Hypoderma* are stimulated to oviposition by bright sunlight and usually egg laying takes place largely in the sunshine. Both species have been observed, however, to deposit eggs in the shade, and occasionally when the sun was fairly well covered with clouds, especially if there were occasional bursts of sunshine. Oviposition rarely takes place when the sky is heavily clouded, and dense shade such as under large sheds appears to be shunned by the females of both species. Females of both *H. bovis* and *H. lineatum* have been observed to be active on days when the temperatures were comparatively low, provided the sun was shining brightly. No doubt in their protected places close to the ground reflected heat and sunshine stimulate them to activity when the general temperatures are very low. In one instance oviposition of *H. lineatum* was observed when the temperature was between 40 and 45° F. The minimum temperature at 7 o'clock that morning was 20.5° F. and the maximum for the day 46° F. at 3 p. m. It is difficult to say just what is the optimum temperature, as large numbers of flies have been observed ovipositing under a wide range of temperature conditions. Females of this species oviposit freely when the temperatures range between 55 and 85° F. provided the sun is shining.

Apparently the range of temperature in which females of *H. bovis* will oviposit is narrower than in *H. lineatum*, although, in localities where both species occur, females of *H. bovis* usually experience higher temperature, since they emerge later in the season.

High winds and even fresh breezes tend to check egg laying of both species. Occasionally, however, the flies will oviposit on windy days when the cattle are standing in the sunshine in protected places.

LONGEVITY OF ADULTS

Owing to the fact that the adults of *Hypoderma* are very restless when in captivity and since there seems to be no means of keeping records of specimens in nature, the writers' observations on the length of life of the adults may give erroneous ideas. The longevity of reared adults of *H. lineatum* is shown in Table 10. It ranged from 1 to 25 days and averaged somewhat longer for males than for females. The markedly greater longevity observed among about 50 adults reared in the laboratory during the spring of 1924 than had been noted previously indicates clearly the probability that certain individuals which emerge prior to periods of uniformly cool weather may live for a considerable time. The specimens referred to were hastened in their emergence by being kept in a warmed room. After emergence the adults were transferred to lantern-globe cages and kept in an unheated room. The temperatures given in Table 10 for these records for 1924 were those recorded in a standard weather shelter out of doors, and hence undoubtedly show a much greater range of temperature than was actually experienced. There is no question but that in nature the flies would seek the sunshine and warmer places which would stimulate activity, and thus we should not expect to find such long periods of existence as those referred to above. The writers' observations in the field also bear out this assumption. It seems certain that when the weather is warm and the adults are active their lives are uniformly very short.

TABLE 10.—Adult longevity of *Hypoderma lineatum* at Dallas, Tex.

Date adults emerged	Num-ber of males	Num-ber of fe-males	Record of death	Lon-gevity	Temperature			Remarks
					Min.	Max.	Aver-age	
1915								
Apr. 12		1	Apr. 19, a.m.	Days 7	°F. 48.0	°F. 83.5	°F. 67.6	In cage 1 foot by 1 foot by 1 foot, with leaves.
Apr. 19		1	Apr. 22, p.m.	3	54.0	82.0	69.0	In small cage, with leaves.
1916								
Mar. 20	1	3	Mar. 21, 2 ♀; Mar. 22, 1 ♀; Mar. 23, 1 ♂	1 to 3	61.5	97.9	80.2	In cage 1 foot by 1 foot by 1 foot in sun.
Mar. 22	10	10	Mar. 23, 1 ♀; Mar. 24, 1 ♂, 2 ♀; Mar. 25, 3 ♂, 5 ♀; Mar. 27, 2 ♀, 1 ♂; Mar. 28, 2 ♂; Mar. 29, 3 ♂	1 to 7	38.0	88.0	61.7	In small and large cages and on cow.
Mar. 27	2	2	Mar. 28, 1 ♀; Mar. 29, 2 ♂, 1 ♀	1 to 2	39.5	88.0	66.3	Do.
1918								
Feb. 25	2		Feb. 27, 1 ♂; Feb. 28, 1 ♂	2 to 3	38.0	97.5	66.2	In laboratory.
Feb. 26	1	5	Feb. 28, 1 ♂, 3 ♀; Mar. 1, 2 ♀	2 to 3	38.0	87.0	58.2	Do.
Feb. 27		1	Mar. 1	2	38.5	87.0	56.2	Do.
Mar. 11	3	1	Mar. 14, 2 ♂, 1 ♀; Mar. 19, 1 ♂	3 to 8	33.7	90.0	60.9	In 1-inch tubes (♀ deposited).
Mar. 13	2	1	Mar. 15, 1 ♀; Mar. 19, 2 ♂	2 to 6	33.7	90.0	56.5	In 1-inch tubes with leaves.
1921								
Mar. 7	8	1	Mar. 14, 2 ♂; Mar. 15, 4 ♂, 1 ♀; Mar. 16, 2 ♂	7 to 9	36.0	87.0	63.4	In lantern globes with leaves.
Mar. 8	8	1	Mar. 12, 1 ♀; Mar. 13, 1 ♂; Mar. 15, 1 ♂; Mar. 16, 4 ♂; Mar. 17, 2 ♂	4 to 9	36.0	87.0	64.0	
Mar. 12	10	8	Mar. 13, 1 ♂; Mar. 15, 1 ♂; Mar. 18, 7 ♂, 8 ♀; Mar. 20, 1 ♂	1 to 8	51.0	87.0	71.7	In cage 1 foot by 1 foot by 1 foot, with leaves.

TABLE 10.—*Adult longevity of Hypoderma lineatum at Dallas, Tex.*—Continued

Date adults emerged	Number of males	Number of females	Record of death	Longevity	Temperature			Remarks
					Min.	Max.	Average	
1921								
Mar. 13	1	2	Mar. 16, 1 ♂, 1 ♀; Mar. 17, 1 ♀	Days 3 to 4	°F. 52.0	°F. 87.0	°F. 71.1	In lantern globes, with leaves.
Mar. 14	6	3	Mar. 16, 1 ♀; Mar. 17, 2 ♂, 1 ♀; Mar. 18, 3 ♂, 1 ♀; Mar. 19, 1 ♂	2 to 5	52.0	87.0	74.5	Do.
Mar. 15	9	2	Mar. 17, 1 ♂; Mar. 21, 5 ♂, 2 ♀; Mar. 22, 3 ♂	2 to 7	43.0	87.0	72.1	In lantern globes, with leaves. Copulated.
1924								
Feb. 7	2	----	Feb. 13, 1 ♂; Mar. 3, 1 ♂----	6 to 25	26.5	82.5	51.25	In lantern globes in cool room. Outdoor temperatures are given.
Feb. 9	2	----	Feb. 27, 1 ♂; Mar. 1, 1 ♂----	18 to 21	26.5	82.5	50.93	Do.
Feb. 14	3	1	Feb. 27, 1 ♀; Mar. 4, 2 ♂; Mar. 8, 1 ♂	13 to 23	26.5	82.5	52.55	Do.
Feb. 16	2	1	Mar. 5, 1 ♂; Mar. 8, 1 ♀; Mar. 10, 1 ♀	18 to 23	25.0	77.5	51.10	Do.
Feb. 18	5	5	Feb. 27, 2 ♂; Mar. 1, 3 ♀; Mar. 3, 1 ♂; Mar. 4, 1 ♀; Mar. 5, 1 ♂; Mar. 6, 1 ♂, 1 ♀	9 to 17	26.5	77.5	50.37	Do.
Feb. 25	5	3	Mar. 6, 1 ♂; Mar. 7, 1 ♂, 2 ♀; Mar. 10, 1 ♀; Mar. 17, 3 ♂	10 to 21	25.0	77.5	49.41	Do.

The longevity of *H. bovis* apparently does not differ much from that of *H. lineatum*. Specimens reared at Dallas, Tex., lived from 2 to 4 days in cages. In Middletown, N. Y., a number of adults were kept in cages in the shade and supplied with green leaves. These lived from 4 to 10 days with an average of 6 days. Specimens of both species captured in nature live in confinement only 1 or 2 days.

SEASONAL HISTORY

There are some distinct differences in the seasonal development of *H. bovis* and *H. lineatum*. These must be considered in control undertakings and they will be pointed out under the several topics following. Both species are essentially single brooded.

SEASON OF ADULT ACTIVITY

Adults of *H. lineatum* appear under usual conditions during the first warm days of spring. The actual date necessarily varies with latitude and altitude as well as with local climatic conditions. It appears that in the southern range of *H. lineatum* the period during which adults of that species are active is longer than in any other portion of the country. Not infrequently in southwestern Texas adults begin to emerge in December and continue to appear during warm periods throughout the winter. In this section the maximum abundance of adults apparently occurs about the middle of February. Observations made by D. C. Parman at Uvalde, Tex., indicate that during some years, at least, adults may continue to appear until about April 1, thus extending the period of adult activity over about four months. At Dallas, Tex., the adults rarely, if ever, emerge be-

fore February 1 or after April 15. The maximum abundance usually occurs between February 20 and March 15. In the plateau region of southwestern Texas in certain instances larvæ have been found to mature early enough in the fall to permit of the issuance of a considerable number of heel flies in the fall. It has not been possible to determine if this really takes place, but the finding of a young larva in the gullet of a cow on January 4 is fairly conclusive proof that some eggs are deposited in October or November. It is certain that some heel flies emerge and attack cattle during December, and heel-fly activity has been observed on numerous occasions in January. The season of adult activity in New Mexico, Arizona, and California appears to be about the same as observed at Dallas. Throughout the central belt of States—that is, between the latitudes 35 and 45° N.—the period of activity is approximately between March 15 and May 1, and in the northern tier of States between April 1 and June 30. These dates are only approximate, and vary much during different years, as well as with altitude and local conditions.

In New York adults of *H. lineatum* may begin oviposition as early as the middle of April, are most abundant during the first three weeks of May, and cease activity about the end of June. In the territory where *H. bovis* occurs it is difficult to determine the date of cessation of activity of the adults of *H. lineatum*, since their seasons of activity overlap.

In New York considerable numbers of adults of *H. bovis* begin to oviposit during the first week in June and apparently some emerge during the latter part of May. The flies are very annoying to cattle during June and the first half of July, are less so during the remainder of July and the first half of August, and during the remainder of August and up to the middle of September only stragglers are abroad. Since normal larvæ have been found in the backs of cattle in New York after September 1, some fly activity is possible throughout that month. No flies have been seen, however, nor have the effects of their attack been noted, after September 14.

Hadwen (36) states that at Agassiz, British Columbia, adults of *H. bovis* appear in the early part of June and continue up to the beginning of August, and that adults of *H. lineatum* were out from April 15 to April 24. Carpenter (19) records the emergence of adults of *H. bovis* in June and July, and deposition of eggs of *H. lineatum* on May 8 and June 16, at Athenry, Ireland.

The season of oviposition of both species is about coincident with that of adult emergence.

SEASONAL DEVELOPMENT OF LARVÆ

Rather abundant data regarding the seasonal occurrence of larvæ of *H. lineatum* in the gullets and viscera of cattle are presented on page 47 and Tables 3 and 4. In general, approximately two and one-half months elapse between the deposition of eggs and the earliest appearance of larvæ in the gullets.

In the vicinity of Dallas, Tex., the larvæ first appear in the submucosa of the gullets of cattle at about the end of March and continue to enter that organ until the maximum is reached during Sep-

tember. There is then a gradual reduction in numbers until about January 1, when all have migrated from the gullet.

In southwestern Texas the larvæ begin to reach the gullets distinctly earlier than at Dallas, thus closely conforming with the earlier appearance of adults in that region. The earliest larva observed by the writers to appear in a gullet was a single specimen 4.2 millimeters in length taken from an animal slaughtered in a Fort Worth, Tex., packing house on January 4, 1924. This specimen evidently developed from eggs deposited the previous fall.

At Herkimer, N. Y., larvæ began to appear in the gullet about the middle of July and the last larvæ left that organ about April 1. Thus it is certain that the larvæ are to be found in the gullets for about nine months.

The seasonal prevalence of larvæ in the subcutaneous tissues of the backs of cattle is closely correlated with the time when the larvæ reach the maximum size attained by them in the gullet, and to some extent with the period of adult activity. Knowledge of this subject is of vital importance in connection with any control procedure, yet the information published is meager in the extreme.

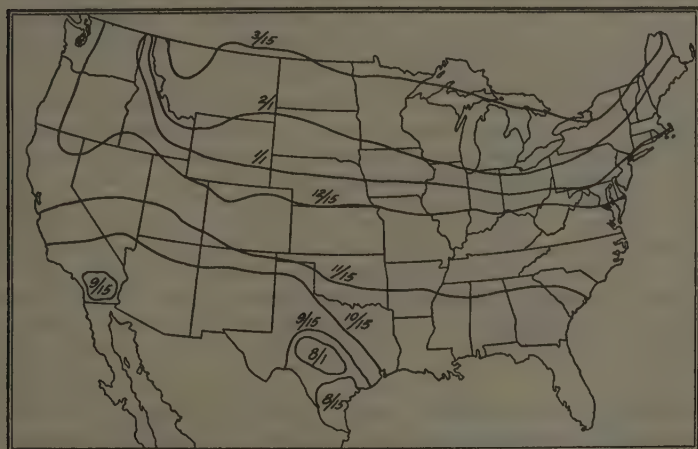
The earliest appearances in the United States of larvæ of *H. lineatum* in the backs of cattle occur in the plateau region of western Texas. On August 10, 1919, at Roosevelt, Tex., O. G. Babcock observed grubs in considerable numbers in the backs of cattle. A few collected on August 12 showed some to be in the early fifth stage. Thus they must have appeared on the backs about July 15. In 1923 fifth-stage larvæ were found by Mr. Babcock at Sonora, Tex., on August 22. These must have reached the backs of the cattle about July 30. At Uvalde, Tex., records made by D. C. Parman during several years show that the first appearance of larvæ in the backs of cattle is later than it is in the plateau region to the north. The earliest appearance noted at Uvalde was on August 12, 1918. The larvæ in this case evidently had been present about 10 days.

Mr. Parman's records at Uvalde indicate that larvæ usually begin to appear under the skin about the middle of September. Some years, however, they may appear as late as October 9, as was observed in 1920. During that season the maximum number present was noted on January 15.

At Dallas, Tex., fairly accurate records of the earliest appearance of larvæ in the subdermal tissue have been made in 10 different years, during the period from 1907 to 1922. These dates have been rather uniform, ranging from about October 10 in 1914 and 1918 to October 30 in 1916. The year 1923 was an exception, as in that year the larvæ appeared about September 8.

At Herkimer, N. Y., the date of appearance of larvæ of *H. lineatum* in the subdermal tissue of the backs of cattle was found in 1920 to be about March 1, and in 1922 about February 6. At Middletown, N. Y., in 1920 larvæ of *H. lineatum* came to the backs about February 12, and in 1923 about February 1. At Watertown, N. Y., in 1920 the date of earliest appearance was about March 3. In Kane County, Ill., C. C. Compton found a single small larva in one of 200 cattle examined on February 7, 1924, thus showing the earliest appearance to be soon after February 1. Subsequent collections made by Mr. Compton indicate that this date is sub-

Hundreds of collections have been made by the writers and by correspondents throughout the country, and with these records as a basis the dates of appearance of the earliest larvæ of *H. lineatum* have been estimated and the accompanying map (fig. 33) constructed. Unfortunately, as the number of accurate records of the time of first appearance is small, many discrepancies will be found, but it



is hoped that the data available will serve a useful purpose in control undertakings and also stimulate others to add to these much needed records.

The date when the first larvæ become mature and leave the host is an important one from an economic point of view. This date is necessarily closely correlated with the date when the first grubs of the season reach the back. It seems extremely rare for these earliest grubs to complete their development in the minimum time, hence the first emergence of larvæ from the cattle should be expected to take place about 45 days after the grubs first reach the back. At Dallas the earliest larvæ become mature and begin leaving the host between December 1 and 15 during average years. The following are the approximate dates when mature larvæ began emerging from cattle at Middletown, N. Y.: In 1920, March 26; in 1922, March 16; and in 1923, March 19.

The time of maximum abundance of larvæ in the backs of cattle varies considerably in different herds and during different years. At Dallas, Tex., this maximum usually occurs, on the average, about January 10, and at Uvalde, Tex., about December 15.

The date when the last grub leaves the cattle varies considerably in different herds, as well as in different localities and during a series of years. This point is of little economic importance for *H. lineatum* in those States where *H. bovis* also occurs, for the latter always persists in the hosts later in the season, and the two species must be dealt with as a unit. At Dallas, Tex., the date when cattle become free from grubs in their backs has been determined during several years. In 1915 this date was March 20; in 1916, April 12; in 1917, March 18; in 1919, March 15; in 1921, March 20; and in 1922, March 16. At Uvalde, Tex., Mr. Parman has observed the cattle to become free of grubs between January 20 and April 12. It is interesting to note that Mr. Babcock found two specimens of *H. lineatum* in the back of a cow at San Angelo, Tex., on March 20, 1924. These larvæ would not have been mature in less than 15 days. Since the grubs of this generation began to appear in the backs of cattle in that region about August 2, there is a remarkable and very unusual period of infestation of the backs of cattle of about eight months. Thus it appears that there is a wider variation from year to year in this respect in southwestern Texas than occurs elsewhere. A very general idea of the time when all larvæ of *H. lineatum* have emerged from the cattle may be gained from the following dates: March 1, southern Arizona and southern California; March 15, Alabama, Georgia, North Carolina, Oklahoma, and southern New Mexico; April 15, Maryland, Missouri, and Nevada; May 1, Pennsylvania, Indiana, Colorado, Idaho, and Washington; June 1, North Dakota and Michigan; June 15, New York and Montana. Observations made by W. E. Dove in 1924 indicate that all larvæ of *H. lineatum* would have left the cattle in the vicinity of Aberdeen, S. Dak., about May 5, and at Minot and Dickinson, N. Dak., and at Moorhead, Minn., about May 10. The season, however, was more advanced that spring than usual. On May 1, 1924, all grubs were found to have emerged from cattle at Sioux Falls, S. Dak.

In general the duration of the infestation of the backs of cattle in *H. bovis* is longer than in *H. lineatum*. This is brought about through the longer developmental period of the larvæ in this situation and the wider spread of time between the date the first larvae of *H. bovis* reach the back and the date the last ones appear there. The writers' records indicate that the earliest larvæ of *H. bovis* reach the subcutaneous tissues from one to two weeks after those of *H. lineatum*. On the other hand, the larvæ of *H. lineatum* arrive in that portion of the host in much larger numbers proportionately during the first month or six weeks following their first appearance.

The writers have checked closely the earliest appearance of larvæ of *H. bovis* in the subdermal tissues, as well as the time of dropping of the last grubs in herds of cattle in New York during three seasons. The earliest appearance of *H. bovis* was February 2 in 1923 in Orange County, N. Y. In 1920 they appeared about February 26, and in 1922 about February 22. At Herkimer they first reached the subdermal tissues about March 8 in 1920, April 15 in 1921, and

February 20 in 1923. The last date on which a third-stage larva was observed to reach the region of the back was June 6, 1922, at Middletown, N. Y. The record of earliest dropping of a mature grub of this species at Middletown was April 11, in 1923. Emergence from the host probably begins rather later than this on the average. In New York the maximum number of grubs of this species in hosts occurs about May 1.

Judging by collections and observations made in other States the seasonal occurrence of *H. bovis* tallies rather closely with that noted in New York. One record of earlier appearance has been made in western Pennsylvania, where in 1916 the grubs reached the back about January 25. That year grubs seemed to have been exceptionally early, especially in the Northeastern States. The dates of earliest appearance in the backs of cattle as calculated from observations and collections in some of the infested territory are as follows: Maine, February 15; New Hampshire, February 8; Vermont, February 20; New Jersey, February 10; Ohio, February 8; Indiana, February 3; Illinois, February 5; Michigan, February 25; Wisconsin, March 2; Iowa, February 15; Wyoming, February 15; Washington, February 8. These dates are presented to give a general idea of the time of earliest appearance of larvæ of *H. bovis* in the subdermal tissues. It is recognized that they are not based on continuous accurate observations and that they will vary in different parts of a State and during different seasons.

The date when all the grubs leave the host has been found to vary widely and in general to be much later than has been supposed. In New York in both Orange and Herkimer Counties most of the grubs are out of the backs of cattle by August 1, but healthy specimens have been taken as late as September 2 in 1922 at Middletown and August 30 during the same year at Herkimer. Collections of *H. bovis* made by W. E. Dove at Aberdeen, S. Dak., on April 21, 1924, indicate that the cattle would be free from grubs in that locality about May 15.

It is worthy of note that the development of grubs in cattle infested in the North and shipped into the South agrees closely with that which occurs in the native habitat of the species. For instance, infested cattle shipped to Miami, Fla., from Syracuse, N. Y., during the winter showed a good infestation of well matured grubs on May 25. Larvæ of *H. bovis* in cows shipped from Michigan to Dallas, Tex., continued to develop and emerge normally up to June 3, when the last one dropped.

In Ireland, Carpenter, Phibbs, and Slattery (19) record the presence of larvæ of *H. lineatum* in the backs of cattle on March 29, and a few larvæ of *H. bovis* were still present on June 10. Lehmann (59) and Vaney (105) found the highest percentage of grubby hides to occur in July in the Lyonnaise region of France.

NATURAL CONTROL

The combined action of all agencies of natural control has a marked effect on the abundance of both species of *Hypoderma*. This is true even in areas where the pest is at its worst.

DESTRUCTION BY BIRDS AND MAMMALS

Birds undoubtedly destroy many larvæ as they drop to the ground after emerging from the backs of cattle. The pupæ also are subject to attack, since they often remain exposed on the surface of the soil or only slightly covered. Several instances were observed in New York in which robins (*Planesticus migratorius*) devoured larvæ of *H. bovis* with avidity. In one case a larva under observation as it burrowed into the soil was seen by a robin sitting on a fence. The robin flew down, picked up the larva, and escaped with it before the bird could be frightened away. This larva was almost covered by the soil as it burrowed in. Species of the larger ground birds undoubtedly destroy many larvæ. Henry Polson of Mountainview, Wyo., makes the following statement: "Sometimes magpies pick holes in the backs of the cattle, trying to get the grubs out, causing sores." In rather extensive observations made by one of the writers in areas where magpies (*Pica pica hudsonia*) abound, this action has not been seen, hence it is thought to be rare.

Many larvæ which emerge from cattle in the barnyards where poultry range are destroyed by fowls. Chickens have been observed to devour greedily considerable numbers of mature larvæ when fed to them.

It is probable that small rodents destroy many larvæ and pupæ. Stegmann (94) states that the pupæ on the ground are destroyed by moles.

INSECT ENEMIES

No predacious insects have been observed to attack the larvæ or pupæ of *Hypoderma* in the United States, and it is thought that they are not an important factor in control.

No parasites have been found in nature, but very few pupæ have been recovered after exposure in fields. The writers have reared a considerable number of specimens of *Nasonia brevicornis* Ashm. from pupæ kept in screen cages in an outdoor insectary, in more or less close association with parasitized pupæ of muscoid flies.

A. Gansser, of the Warble Committee of Switzerland, states in a letter that he thinks that a hymenopterous parasite which has not been determined is an important factor in control in that region.

FUNGOUS GROWTHS

The writers have observed the growth of molds on and in the puparia of *Hypoderma*, and there is some reason to believe that the insects may be attacked in some cases. Lucet (63) expresses the opinion that in France certain fungi destroy the pupæ.

EFFECT OF SUBMERGENCE ON LARVÆ AND PUPÆ

In 1921 a considerable number of extracted larvæ of *H. lineatum* were submerged in water for periods ranging from 3 to 23 hours. These periods apparently had very little effect on the larvæ; at least the percentage found dead at the end of three days was not greater than in the untreated groups. During 1922 five mature larvæ were submerged from 1½ to 19 hours. The larva submerged the shortest period produced an adult in normal time, but the four submerged

6½ to 19 hours failed to transform. In 1924 six larvæ which had emerged normally from a host were submerged in lots of two for 24, 30, and 40 hours. Adults emerged from all of these in normal time. Two pupæ were also submerged for 30 hours and both transformed to adults.

Six mature larvæ of *H. bovis* were submerged in water for periods ranging from 49 to 122 hours. All except one, which was submerged for 121 hours, produced adults in about the normal length of time.

From these tests it is clear that these stages are not easily drowned, and this might enable them to survive carriage for considerable distances by flood waters.

CLIMATIC CHECKS

Climatic conditions undoubtedly have a marked effect on the distribution and abundance of Hypoderma. The relationship between climate and the distribution of the two species of Hypoderma has been discussed in a general way under the heading "Distribution."

One of the writers (4) has made the statement that he believes that climatic barriers have prevented the general dissemination of *H. bovis* throughout the United States. He says,

One explanation of this possible barrier will be found in the fact that *H. bovis* is generally later in emerging from the backs of cattle than *H. lineatum*. The grubs emerging from the backs of cattle shipped to the Southern States would, on account of their later emergence, encounter excessively hot weather, and this may account in part at least for the failure of the species to establish itself in the warmer portions of the country.

No facts appear to have come to light since the publication of the foregoing statement which would tend to disprove this conclusion. *H. lineatum* establishes itself in new sections with less difficulty, and uninfested areas are less general with this species. It must be recognized, however, that meteorological conditions are potent factors in limiting its abundance as a parasite of cattle.

Climatic conditions appear to have very little direct effect upon the development of the grubs within the host. Climatic influences are therefore restricted to the portion of the year when the insects are separated from their hosts; that is, while they are in the pupal and adult stages.

Among the several meteorological factors which affect Hypoderma, rainfall and humidity during the pupal and adult stages are probably the most important. It has been found that where the soil beneath pupæ is kept very moist the mortality is extremely high. Under such conditions some of the insects appear to die before development has proceeded very far, and others transform to adults but are unable to escape from the puparia. This appears to be due to the large size of the abdomens, which are not reduced sufficiently through evaporation to allow them to be withdrawn from the puparia. Heavy rains coming at the time the adults emerge may destroy many of them, and continuous rainy or even very cloudy weather after the emergence of the adults will prohibit oviposition. Since the longevity of the flies is limited, adverse weather conditions of comparatively short duration will prevent individuals from ovipositing. Owing to the fact that large numbers of flies usually

emerge at approximately the same time, regardless of the time the pupæ may have been formed, rainy weather immediately after emergence of one of these large groups of flies may affect materially the infestation of the following year.

Clouds have been mentioned as being a factor in repressing oviposition. Their influence is felt only by the adult insect, as cloudy weather in the absence of unusual precipitation does not seem to affect the development of the pupæ, except possibly to prolong slightly the pupal stage.

Winds apparently have a double influence: In the first place they cause a more rapid drying of the surface soil, which would benefit the pupæ; and secondly they have an adverse effect upon oviposition, since the flies, especially those of *H. lineatum*, will not oviposit freely in a strong wind. This influence is less potent than the others, however, since it is not so generally operative. Cattle congregated in places protected from the wind are frequently attacked by heel flies.

Temperature conditions probably rank next to precipitation in their effect on these species. Periods of unusually warm weather in the winter or early spring often tend to cause the emergence of flies which are destroyed by succeeding days of cold or rainy weather.

As is generally known, warm bright days are most favorable for the activity of *H. lineatum*. It is probable, however, that during periods of high temperature, that is, when the daily maxima run above 95° F., the total number of eggs laid by a fly is reduced. When such higher temperatures are reached, oviposition occurs mostly before the hottest part of the day. The destructive effect of the direct rays of the sun on both *H. lineatum* and *H. bovis* is apparent when caged flies are placed in the sun during moderately warm weather. They become very active and fly most of the time, soon weakening and falling to the bottom of the cage where they die, sometimes very suddenly.

Oviposition of *H. lineatum* takes place at surprisingly low temperatures if the sun is shining. Often adults are active during the day when the minimum temperature in the morning ranges between 19 and 22° F. Flies have been observed to oviposit when the temperature was as low as 45° F., the maximum temperature for the day being 46° F. There seems to be no doubt that heat is an important factor in restricting the southern spread of *H. bovis*.

Mature larvæ and pupæ can withstand rather low temperatures. The pupæ appear to be more resistant to cold than the larvæ. A considerable number of observations have been made by the writers on the effect of cold on these stages of *H. lineatum* at Dallas, Tex., but the minimum fatal temperature has not been determined with accuracy. In 1918, when a minimum temperature of 3.5° F. was reached, the larval and pupal transformations of a number of specimens was under observation. Considerable protection was afforded these and a good percentage of adults emerged. Among a number of larvæ and pupæ exposed to 9.5° F. an adult emergence of 54.5 per cent was secured. In other series of specimens which experienced minimum temperatures of about 19° F. approximately 68 per cent produced adults. This is not much below the percentage of emergence under outdoor conditions where the temperatures do not drop

below freezing. A mature larva of *H. lineatum* placed in a freezing room for 24 hours at a temperature of about 7° F. failed to pupate, whereas a fresh pupa exposed in the same way produced a normal adult. Nine mature larvæ of *H. bovis* subjected for from 24 to 26 hours to temperatures in a freezing room of 7 to 9° F. failed to pupate. Five larvæ of this species placed in the room at 25 to 29° F. for 26 hours gave an adult emergence of 80 per cent, and five larvæ kept at from 32 to 33° F. for 14 days pupated promptly upon removal and 60 per cent emerged.

SOIL CONDITIONS AND DRAINAGE

Naturally soil character and drainage are linked with rainfall in their relationship to Hypoderma. The writers' observations indicate that porous, well-drained soils are more favorable for Hypoderma than heavy, flat-lying lands.

In the valley of the Red River of the North, where Hypoderma seldom occurs, there is probably a soil condition which prevents fully developed larvæ from producing adults. It is known that animals infested with Hypoderma have been shipped into that section, but the pest has never become well established.

HOST RESISTANCE AND OTHER CONTROL FACTORS

The great disparity in the number of grubs found in different cattle in the same herd is well known. The writers' investigations indicate that this difference in degree of infestation is brought about by a combination of several causes. Probably the main reason why one animal will show a heavy infestation of grubs while another will be free from grubs or comparatively so, is that there was a marked difference in the number of eggs which were attached to them. The reason why one animal may receive a much larger number of eggs than another, however, is not altogether apparent. Certainly the element of chance enters here strongly. The individual idiosyncracies of the animals are also factors. Some animals seem more able to detect the presence of flies than others and secure protection from them.

A large series of observations made on individual animals year after year shows that the extent of infestation may vary greatly. The writers have found, however, that certain animals are uniformly resistant to the grubs from the time the eggs hatch to the time the larvæ complete their development or die within the host. This individual resistance is probably due in a large measure, as pointed out by Hadwen (35, 40), to eosinophilia. That there is a very definite reaction against the larvæ is apparent when they penetrate the skin of such resistant hosts. The exudate at the point of entrance is usually more profuse than ordinarily, and the infiltration of the connective tissue beneath is pronounced. Apparently this strong reaction against the invading parasite is present throughout its course in the body of the animal. It is after the larvæ have reached the subcutaneous tissues of the back, however, that the destruction of the larvæ is most apparent. The reaction against the larvæ appears to differ considerably in different hosts. In some, large swellings occur; in others, the reaction seems to be

more localized. In the latter case there is a tendency for the skin to close the grub opening and cut off its air supply. In certain animals there is also a strong tendency to form pus in and about the cyst, and in such cases the grubs usually die. The writers' observations show that the mortality in the subcutaneous tissues of the back is very high. Their figures indicate that 60.5 per cent of those which have cut holes through the skin die before reaching maturity. Of this percentage approximately 16 per cent succumb in the third stage, 46 per cent in the fourth stage, and 38 per cent in the fifth stage. It appears also that occasionally third-stage larvæ which reach the subdermal tissues die before they succeed in cutting through the skin.

There is a marked difference in the degree of infestation of animals of different ages. Young stock, notably animals from 1 to 3 years old, almost always show a higher percentage of infestation than mature animals. There is also some reason to believe that as cattle become very old the degree of infestation is again increased. Seymour-Jones (91) advances the theory that in young stock the tenderness of the muscle (*panniculus carnosus*) immediately under the skin enables the grubs to penetrate them, whereas in older cattle they do not all get through.

Hadwen (35, 40) is of the opinion that the difference in degree of infestation between young and matured animals may be explained by a gradual development of immunity following the repeated attacks of parasites. He believes that a first invasion of parasites in an unresisting host stimulates the production of both antistances and eosinophiles to neutralize their cast-off products, and in addition to this, that there must be a third substance which is antagonistic to the parasites themselves; he believes that this substance is secreted by the eosinophiles, and that it paralyzes or kills the parasites which are surrounded by the eosinophiles in the tissues.

The writers believe that the difference in the number of grubs found in young and old cattle may be explained in part by this reaction, but that other factors enter into the question. In general, young animals are more exposed to the attack of the flies, both because they are not housed so long in the spring and because they are seldom placed in barns during the time when the flies are ovipositing. It is also true that the young stock are frequently not as well fed as the older animals. The statement is made frequently by dairymen and stockmen that poor animals are more heavily infested than fat ones. The writers have observed many instances in which very fat animals were fairly well infested with grubs, but their observations indicate that the poor cattle are usually more heavily infested. It appears logical to believe that well fed, healthy animals have more natural resistance to grubs than those in poor flesh and with lower vitality. It is also certain that cattle in an extremely impoverished condition will fall more ready prey to the flies at the time of oviposition. It seems evident, however, that the presence of a large number of grubs, especially in cattle not receiving an optimum amount of feed, will reduce flesh condition.

No marked difference in susceptibility seems to exist in different breeds. When water or shade is readily available it serves as a means of partially protecting from infestation the stock which have

access to it. Large numbers of grubs and pupæ are destroyed by the walking of the cattle, especially in pastures where the animals are concentrated.

ARTIFICIAL CONTROL

In considering control or eradication it should be borne in mind that the flies do not feed, nor have any habits been noted which could be utilized in accomplishing their destruction. The flies also do not seem to be sensitive to the presence of foreign materials on the host, and therefore are not easily repelled. The egg stage is comparatively short, hence any treatment directed against it must be applied frequently. During the greater part of the year the larvæ are protected within the body of the host; that is, from the time of penetration immediately after the hatching of the eggs to the appearance of the third-stage grubs in the subdermal tissues of the back. There is, however, a rather definite period, usually not exceeding four months, during the fall, winter, and spring, varying according to latitude, during which the grubs are localized in the backs of the cattle where they may be reached through the apertures in the skin. The fact that both species are practically incapable of developing in hosts other than cattle is also a point of distinct advantage in any control procedure attempted.

POSSIBILITIES OF CHECKING THE SPREAD OF HYPODERMA

No effort has been made in this country to check the spread of either species of *Hypoderma*. In fact *H. lineatum* appears to have long since established itself in all parts of the United States where it is capable of existing. *H. bovis*, on the other hand, is much more restricted in distribution and it appears that it is capable of becoming much more widely disseminated in this country.

It is probable that *H. bovis*, which at this time occurs west of the Mississippi River only in scattered localities in the Northern States, may cover that region solidly and extend its range well south along the mountain ranges. Hewitt (42, 43, and 44) and others have stated that *Hypoderma* appears to be increasing in abundance in Manitoba. The importance of *H. bovis* as a cattle pest is sufficient to warrant serious consideration of ways and means of checking its spread in this country. It may not be advisable to take legal steps to meet the situation, but certainly stock raisers should recognize the danger of bringing cattle infested with *H. bovis* into regions where that pest does not exist, and take due precautions to destroy all grubs which reach the subcutaneous tissues of the backs during the spring and summer following the arrival of the cattle. Certain uninfested foreign countries have enacted legislation designed to prevent the establishment of *Hypoderma*. Australia (2), for instance, has a law prohibiting the introduction of cattle from the United States, the British Isles, and other infested countries except during the period from December 1 to May 31. Present knowledge of the seasonal history of *Hypoderma* shows clearly that such a restriction would not give a complete protection against the introduction of the pests. It would appear, however, that some system by which the animals could be kept under surveillance and all grubs destroyed during the period of one full year after importation would be effective.

EFFECT OF BURIAL ON LARVÆ AND PUPÆ

It is difficult to say just what degree of control is effected through plowing. From reports on the abundance of grubs in cattle in the Central States in the eighties as compared with the number of grubs in the same regions now, it appears that there has been a decrease in abundance. Many think that the restriction of pastures to comparatively small areas and more general and intensive cultivation are largely responsible for this. It is reasonable to suppose that plowing fields where larvæ and pupæ occur would destroy many of them.

Several mature larvæ and freshly formed pupæ of *H. lineatum* were buried in sand and black clay soil, at depths of from $2\frac{1}{4}$ to 4 inches. In most instances the larvæ worked their way to the surface in a short time and pupated on top of the soil. In the black clay the flies emerged in about the normal time and pushed out of the soil even when the pupæ were buried to a depth of 4 inches. In the fine sand, however, the flies were found to have emerged and worked upward about half an inch from the puparia, where they died and were found later with a comparatively hard cell of sand formed around them.

Many larvæ in pastures undoubtedly become covered with manure, as are those that drop in barns and are shoveled out with the dung. To test the effect of burial under such conditions four mature larvæ were placed on a board and a large fresh cow dropping was laid on them. None of them moved from where they were placed. Three of them died without pupating and the other died as a half-developed fly. This preliminary test probably indicates that burial in fresh cow manure is very destructive and that many larvæ are destroyed in this way, since often a large percentage of the grubs leave the hosts in the barns.

Some larvæ of *H. bovis* buried from 1 to 6 inches in both clay and sand came to the surface, while others pupated near where they were buried. Some flies emerged from pupæ buried to a depth of 6 inches, but apparently the burial below 3 inches was detrimental, especially if the soil was very moist.

PROTECTION OF CATTLE BY HOUSING AND NATURAL BARRIERS

There are abundant examples of the great reduction of infestations effected by housing the herd during the periods of fly activity. Some dairymen leave their barns open or provide sheds which the cattle can enter when attacked by the flies. The flies, however, have considerable opportunity to deposit eggs on the cattle before they can get into the buildings. Such an arrangement has the advantage of allowing the cattle to escape from continued annoyance and fright, which is inevitable when no protection is afforded. Since the flies will oviposit in the broken shade supplied by trees, the presence of woods in a pasture will not greatly reduce infestation, but is beneficial in that the worry to the cattle is lessened. Streams afford effective protection against *H. lineatum*, but less against *H. bovis*. The excitement, however, is greatly relieved and milk flow maintained when cattle have access to streams or ponds. There is danger of some injury to cattle, however, from standing in mud and water for long periods when weather is favorable for continued fly activity.

The construction of sheds is advisable where they will perform the double service of protecting the stock against heel flies and from adverse climatic conditions.

REPELLENTS AGAINST HEEL FLIES

For many years various ill-smelling applications have been used with the view of protecting cattle from the attack of heel or warble flies. Prior to the last few years, during which our knowledge of the life history of these pests has clearly showed that the eggs are not deposited on the backs of the cattle, it was the custom to use various repellent smears and washes upon the backs of cattle. As it is now known that the eggs are deposited largely on the legs and lower portions of the body, the futility of this practice is at once evident. Inquiry into the results of the application of fly sprays has led the writers to conclude that the claims that they are efficient against grubs are unfounded.

The fact that the adults of *Hypoderma* do not partake of food would suggest that their reaction toward attractant and repellent chemicals or other substances would be less than in those species which have the senses developed to aid them in finding food or breeding places. The writers' experiments and observations along this line seem to bear out this conclusion. It appears probable that the application on the animals of materials which tend to cover the hair or mat it together may affect oviposition more than those materials possessing various odors supposed to be repellent. The experiments in this field, however, have not been sufficiently extensive to enable final conclusions to be drawn.

During 1919 a dairy herd of 61 animals was used in tests of the application of repellents and solvent solutions, as follows: 2 per cent compound solution of cresol, 10 per cent solution of acetic acid, undiluted fuel oil (petroleum), and a mixture of 1 gallon of fish oil with 1 pint of commercial pine tar. These materials were applied to the legs of cattle, some with a spray pump and others with a brush. The applications were made at about 4-day intervals during the period when heel flies were active. While the treatments were being administered heel-fly eggs were found on several of the treated animals. Some were even present on the legs of those treated with petroleum, and on those treated with a mixture of fish oil and pine tar.

Observations made incidentally in the experiments discussed under "Destruction of eggs or larvæ by the use of wading vats" indicate that the application of 2 per cent coal-tar creosote dips at 4-day intervals has no marked effect in repelling flies. The same is true of wading-vat experiments with arsenical solutions.

On a number of occasions where cattle waded and got their feet and legs well covered with mud the flies were found to deposit their eggs freely on the legs above it. The application of gummy materials to the entire animal has not been tried, but this would hardly seem feasible from a practical viewpoint.

DESTRUCTION OF EGGS OR LARVÆ BY THE USE OF WADING VATS

The fact that a considerable percentage of the eggs of *Hypoderma* are laid on the lower legs at once suggests the possibility of destroy-

ing the eggs or young larvæ as they hatch, by applying insecticides to those portions. One of the most convenient and effective methods of accomplishing this is through the utilization of shallow vats. In 1918 experiments were begun to determine the effect on the infestation of dairy cattle of the use of standard arsenical solution. One-half of the cows in a dairy herd was allowed to pass through a wading vat containing the solution about 1 foot deep, at intervals of four days. The other half of the herd was not treated, being kept as a check. In the first year's test 16 cows were treated and the following season these were found to be infested to almost identically the same degree as the 16 cows which were not treated. In 1919 the same herd was utilized in a test under similar conditions, a standard sodium arsenite solution containing about 19 per cent arsenic trioxide being used in the vat. The following season the dipped cows had an average infestation of 7.18 grubs per animal and the untreated cows showed an average of 5.65 grubs per animal. During the spring of 1920 the same herd was again utilized in the same way, except that 18 cows were treated. For charging the vat in this experiment a commercial arsenical dip was used which in concentrated form was said to contain about 9 per cent of cresol salts. In the first two treatments the strength of the solution was about 0.19 per cent arsenious oxide. Subsequently this was raised to approximately 0.22 per cent. The following spring the treated cattle showed an average infestation of 2.5 grubs per head and the untreated ones an average infestation of 3.33 grubs each. During the spring of 1919 another dairy herd was utilized. Thirteen cows representative of the herd in age and breeding were passed through a wading vat at 4-day intervals and 14 cows were utilized as a control. In this case the vat was charged with a commercial coal-tar creosote dip diluted to about 2 per cent. The following season a careful check of the grubs in the treated cattle showed an average of 6.58 per animal, and the untreated animals showed an average of 3.84 grubs each. The following year a similar test was carried out at the same dairy. A count of the grubs present in the treated and untreated groups made on December 30 showed an average of 6 per animal in the case of the former group and 8.14 in the latter. In a subsequent examination made on February 7, the treated animals showed an average infestation of 2.75 grubs each and the untreated animals an average of 2.67 each.

It is possible that better protection would be afforded should the dipping be done every day. It would not be feasible, however, to dip so frequently with the strengths of solutions used and endeavor to cover a greater portion of the legs by having the solution deeper in the vats. In the experiments mentioned, the walking of the cows through the vats, which were 10 feet long at the bottom and 18 feet long at the top, brought the material into contact with the legs considerably higher up than the actual depth of the dip (1 foot). In fact it was found that the udders and bellies of the cattle were fairly well drenched, especially on the cows that were inclined to hurry through the vat.

Imes and Schneider (48) have published results of tests with the application of used automobile cylinder oil, sodium silicate, and coal-tar creosote dip by spraying and wading the cattle through vats

similar to those used in the experiments described above. They concluded that the treatments had a very material effect on the infestation the following season. Since only 10 animals were used in the test the great variation in the degree of infestation may readily be due to causes other than the effect of the treatments. Subsequent experiments conducted by the Bureau of Animal Industry, however, are said to show that a satisfactory degree of control may be brought about in range cattle through the use of wading vats (68).

Studies of the distribution of the eggs of both species of Hypoderma made by the writers show that a large percentage of the eggs are deposited elsewhere than on the legs. This is particularly true with *H. bovis*, which deposits many eggs above the hock joint. It is also the case with the deposition of eggs on dairy or quiet farm cattle by *H. lineatum*. As has been pointed out in preceding pages, the flies often approach such cattle while lying down and deposit large numbers of eggs on the escutcheon, tail, and elsewhere, all of which would be unaffected by dips applied in wading vats.

LABORATORY TESTS OF DIPS ON EGGS OF HYPODERMA LINEATUM

Several authors have suggested the use of sprays or washes containing materials designed to dissolve the attachment of eggs of certain species of Oestridae. Acetic acid is one of those which has been advocated for this purpose. Tests were conducted during 1919 in which eggs of *H. lineatum* were submerged in a 10 per cent solution of acetic acid for periods varying from 3 minutes to 5 days. Following this treatment the eggs were allowed to dry for periods ranging from 30 minutes to 13 days, and then the firmness of attachment of the eggs to the hairs was tested by scraping and pulling them with a dissecting needle or forceps. In every instance the eggs were found to be firmly attached. In most cases the eggshells would tear in two without their attachment to the hair being disturbed.

Hairs bearing eggs of *H. lineatum* were also submerged for a few seconds in 2 per cent coal-tar creosote dips and kept in incubators to determine if the eggs would be destroyed. In one of these tests 29 eggs were submerged three times for an instant in 2 per cent creosote dip at 3 p. m. and then placed in an incubator at 90° F. The following morning one larvæ had hatched and was very active. During the day a total of 21 larvæ hatched from these eggs and were apparently normal. Twenty eggs from the same lot mentioned above were given three dippings as in the previous lot and on the following morning they were again dipped in 2 per cent creosote dip and returned to the incubator. These did not begin hatching until the afternoon of March 25, a full day later than those in the previous lot which were submerged but once. Sixteen or seventeen larvæ, however, hatched from the 20 eggs and all were apparently normal. Another series of 26 eggs which were about one-half through their normal period of incubation were dipped in a 2 per cent solution of a coal-tar creosote dip and placed in an incubator. From these, 19, or 73.08 per cent, of the eggs hatched normally. In still another test 34 eggs were dipped in 2 per cent creosote dip before they were due to hatch. An hour later 10 larvæ had hatched and were active. No other larvæ emerged, thus making a hatch of 29.4 per cent, whereas in a check lot the hatch was 31.3 per cent.

In 1923 two series of tests were made. In the first of these 192 eggs deposited April 10 on cow hair were divided into four lots, each of which was kept in an incubator at about 90° F. The check lot contained 99 eggs. These began hatching on April 13, and 45 per cent of them hatched. The other three lots were submerged for one minute after they had been incubated for 1 hour, 25 hours, and 49 hours, respectively. The respective percentages of larvæ which hatched in these three lots were 42, 45, and 57.5. All of these lots began hatching on the same date as the check.

The second series contained 74 eggs deposited on April 11, 1923; 18 of these were submerged for three minutes in a 2 per cent solution of a coal-tar creosote dip on April 13. These began hatching in the incubator on April 14, and 44 per cent of the larvæ emerged. The other eggs were kept in an incubator except for the time required to submerge them for one minute in crank-case oil, drained from an automobile. Of the 22 eggs dipped immediately after oviposition none hatched, of the 23 eggs dipped 24 hours after being laid 26 per cent hatched, and of the 11 submerged 65 hours after oviposition none hatched.

ATTACK DIRECTED AGAINST HYPODERMA LARVÆ IN THE BACKS OF CATTLE

A number of facts point to the practicability of combating this pest by destroying the larval stages while in the subcutaneous tissues of the back. Control by this procedure is favored (1) by the fact that the species confine their attack almost entirely to cattle, (2) by the fact that there is a rather definite and somewhat restricted seasonal occurrence of the larvæ in that situation, (3) by the presence of an aperture through the hide immediately over the grub during its entire existence in the subdermal tissue, and (4) by the fact that the larvæ are limited in their distribution to the back of the host between the withers and tail. In order to proceed intelligently against the species in this situation it is necessary to have very definite information regarding its seasonal occurrence in the subdermal tissues in each section where control work is undertaken, as also a knowledge of the developmental period in the subcutaneous tissues, particularly as to the minimum time required.

The possibilities of attacking the species in this situation appear to have been recognized in a general way many years ago. Work along this line, however, has been of a very superficial and sporadic nature, with the exception, perhaps, of that carried on in certain districts in Denmark (6), Holland, and Germany (67 and 77.)

EFFECT OF MATERIALS ON LARVÆ REMOVED FROM HOSTS

In order to determine the toxicity of various insecticides and other materials to the larvæ of *Hypoderma*, a series of tests was carried out in which larvæ in different stages of development were removed from the backs of cattle and submerged in these materials. This method of testing the insecticidal value of various chemicals is open to objection, owing to the fact that the conditions are abnormal. Another objection to the use of larvæ extracted from hosts is that practically none of them will produce adults even though

kept under the most favorable conditions, hence there is difficulty in determining the percentage of mortality chargeable directly to the treatment. The tests made show clearly, however, that *Hypoderma* larvæ, especially in the later stages of their development, are very resistant to contact insecticides. In these tests some 25 or 30 different materials were used. Those were selected which would seem to be adapted to use in the destruction of grubs in the cysts in the backs of the hosts. The period of submergence in most cases was about two minutes.

Mention will be made of only a few of the results obtained, since it appears impractical to determine by this method the efficiency of the various materials when applied to the warbles in the cysts. In these experiments it appeared that the saponified coal-tar creosote products gave the highest percentage of mortality within the first 24 hours. Tincture of iodine U. S. P. also gave a high percentage of kill soon after treatment. Certain other materials such as iodoform with neutral carriers and 5 per cent solutions of silver nitrate destroyed a high percentage of the grubs but the action was slower. To illustrate the resistance of the larvæ to the action of certain insecticides it might be mentioned that submergence for two minutes in such materials as crude petroleum and spirits of turpentine killed a comparatively small number.

APPLICATION OF MATERIALS TO GRUBS IN THE BACKS OF CATTLE

Many years ago the application of various smears to the backs of cattle was advocated by many, including such authorities as Ormerod (71) in England. The object in view, however, was not the destruction of the larvæ in the subcutaneous tissues but the prevention of infestation. In connection with their work the present writers have learned of the use by farmers and dairymen of the injection of such substances as kerosene oil and turpentine into the cysts for the purpose of destroying the grubs. Some men have practiced this method for years and are well pleased with the results. In Germany the warble commission (67) advocated the application of birch tar oil to the grubs individually in the backs of cattle. In Ireland and England, as a result of experiments carried out by Carpenter (18), the application of a tobacco decoction in the form of a wash has been advocated. Rène (81) advises, among other methods of control, the injection of 1 cc. of tincture of iodine into the warble.

Attempts to employ gas against the grubs in the backs of cattle have been reported on by Greve (31) and Duncan, Hewitt, and Jardine (28). The results were not encouraging.

In their own work, experiments along these lines have been carried out by the writers on a rather extensive scale since 1918. Most of these tests have been conducted in a way which made it possible to secure accurate records on the percentage of grubs destroyed by the various treatments. In this work various dairy herds were utilized in the vicinity of Dallas and other points in Texas, in Peoria, Ill., and in Orange and Herkimer Counties, N. Y.

Three different classes of materials were employed—powders, ointments, and liquids. The powders were usually applied directly into the grub holes by means of a shaker can. The ointments were in

most cases applied with the fingers, care being taken to press some of the material into the apertures in the skin (fig. 34). The liquids were applied with hypodermic syringes, a blunt needle being used and care being taken not to injure the grub; with oil cans (fig. 35); with eye droppers; or in the form of a general wash thoroughly applied to the backs of the cattle with a stiff brush. In preliminary tests with all of the materials the cattle were numbered and a diagram made of the distribution of the grubs on the back, each grub being numbered and the stage of development determined before the application was made. In some instances the hair was clipped from around the openings in the hide; but the results in each case were checked afterwards by the treatment of other infestations in



FIG. 34.—Applying ointment to grubs in back of heifer

which the hair was left undisturbed immediately around the holes and the position of the grubs marked by clipping the hair below each of them. In injecting the materials into the cysts an effort was made to fill the cavity around the grub with the liquid. The average quantity used was something less than 1 cubic centimeter per grub. In order to determine the results of the treatment in the early experiment, each grub was carefully examined from four to six days after the treatment was made. Then the larvæ were extracted and notes made on their condition and the condition of the lesions produced by them. Following the preliminary tests, large numbers of grubs were treated without determining the stage they were in or otherwise interfering with them before the application. The percentage of mortality in some cases was determined merely by continued observation

of the larvæ *in situ*. In such cases the observations were continued for several weeks to determine the effect on the host of the destruction of the grubs by this method. In order to make accurate observations on the killing power of the various materials used, most of these were administered after the major part of the grubs had reached the fifth or last stage. In most cases a sufficient number of grubs were in the younger stages so that the effect of the various materials upon them could be determined. The tests indicated that, although the younger stages may be more susceptible to the action



FIG. 35.—Injecting Hypodermis cysts with chemicals by means of an oil can

of the insecticides, in those stages they are probably more protected against the materials, since the apertures in the skin are usually much smaller.

Most of the tests in which the results were carefully checked are given in Tables 11 and 12. It will be observed from a study of the results that a number of the materials will produce a mortality above 80 per cent. The writers are of the opinion that materials which will not accomplish the destruction of at least 80 per cent of the grubs present should not be considered as practicable. On the other hand, some of these materials which gave a very high percentage of destruction are not adapted to use in general practice on account of the cost.

TABLE 11.—Treatment of *Hypoderma lineatum* in the backs of cattle, Dallas, Tex., 1918-1924

Material and strength	How applied	Number of cows treated	Number of grubs treated	Number of grubs killed			Number of grubs not killed			Number of grubs doubtful			Number of grubs gone			Percentage killed based on dead and alive
				Stage			Stage			Stage			Stage			
				3	4	5	3	4	5	3	4	5	3	4	5	
Argyrol, 10 per cent solution	Dropper, in hole	2	6	0	0	6	0	0	0	0	0	0	0	0	0	100.00
Arsenical solution, 0.182 per cent As_2O_3	Syringe, in hole	17	57	0	0	3	0	0	28	0	0	21	0	0	5	9.98
Arsenical solution, 0.222 per cent As_2O_3	do.	14	28	0	0	7	0	0	3	0	0	16	0	0	2	70.00
Do.	Wash on back	2	61	0	1	0	0	31	29	0	0	0	0	0	0	1.65
Do.	Wash, 2 applications, 2 days apart.	14	100	2	10	11	0	21	56	0	0	0	0	0	0	23.00
Arsenical solution, 0.237 per cent As_2O_3	Wash on back	7	39	0	0	1	0	0	36	0	0	0	0	0	2	2.70
Benzol, 90 per cent	Injected with oil can	8	115	0	11	88	0	1	5	0	0	0	0	0	10	94.29
Benzol, 100 per cent	do.	56	240	0	31	189	0	8	0	0	3	0	0	9	9	96.49
Borax, saturated solution	Injected with syringe	13	72	0	0	3	0	6	20	0	18	16	0	0	9	10.34
Boracic acid, saturated solution	do.	12	63	0	0	3	0	10	23	1	9	9	0	0	8	8.33
Carbulated petrolatum, 1½ per cent	Pressed into holes	5	62	1	0	4	131	25	0	0	0	0	0	0	0	8.06
Carbon tetrachloride	Injected with oil can	71	375	0	31	298	0	8	1	0	10	0	2	25	97.63	
Chloroform, C. P.	Injected with syringe	6	24	0	0	16	0	0	0	0	8	0	0	0	0	100.00
Copper sulphate, saturated solution	do.	10	59	1	1	31	0	1	0	5	20	0	0	0	0	97.06
Carbolic acid, crude, 1 part; paraffin oil, 10 parts.	Injected with oil can	11	65	0	5	20	0	2	26	0	0	0	0	12	47.17	
Creosote oil (wood)	do.	23	77	0	4	25	0	0	28	0	0	0	0	0	20	50.88
Creosol compound, U. S. P., 1 part; water, 10 parts.	do.	9	52	0	0	19	0	0	7	0	7	19	0	0	0	73.08
Creosol compound, U. S. P., 1 part; water, 5 parts.	do.	7	122	0	2	16	0	3	65	0	0	0	0	0	36	20.93
A creosol compound, 1 part; water, 10 parts.	Injected with syringe	45	136	0	12	91	0	1	18	0	2	3	0	0	9	84.43
Do.	Injected with oil can	8	19	0	0	12	0	0	7	0	0	0	0	0	0	63.16
Do.	Injected with syringe	15	79	0	4	54	0	0	7	0	5	9	0	0	0	89.23
A creosol compound, 1 part; water, 5 parts.	Injected with oil can	17	185	1	19	108	0	0	33	0	0	0	0	0	24	79.50
Creosote dip (coal-tar), 1.66 per cent solution.	Wash on back	18	115	1	9	1	78	0	0	0	0	1	28	10.34		
Creosote dip (coal-tar), 8 per cent solution.	Injected with syringe	6	46	0	5	27	0	0	2	0	2	10	0	0	0	94.12
Creosol ointment, full strength	Pressed into holes	12	90	0	2	51	0	0	7	0	1	29	0	0	0	88.33
Derris extract (proprietary), 1 part; water, 10 parts, plus 4 ounces soap per gallon.	Injected with oil can	15	97	0	14	81	0	0	0	0	0	0	0	2	100.00	
Derris extract (proprietary), 2 per cent in water, plus 4 ounces soap per gallon.	Wash on back	18	108	0	6	7	0	3	80	0	0	1	0	0	11	13.54
Derris powder, dry	Dusted into hole	22	133	0	7	110	0	0	6	0	2	1	0	0	7	95.12
Derris powder, 1 part; paraffin oil, 5 parts.	Injected with oil can	9	24	0	5	19	0	0	0	0	0	0	0	0	0	100.00
Derris powder, 1 part; petrolatum, 2 parts.	Pressed into hole	76	234	1	220	15	0	0	0	0	0	0	0	8	97.77	
Derris powder, 1 part; petrolatum, 5 parts.	do.	21	82	0	3	76	0	0	1	0	0	0	0	2	98.75	
Derris powder, 1 part; petrolatum, 10 parts.	do.	33	123	5	41	66	0	0	3	0	0	1	0	0	7	97.39
Derris powder, 1 part; petrolatum, 15 parts.	do.	15	92	2	43	40	0	0	3	0	0	2	0	0	2	96.59
Derris powder, 1 part; petrolatum, 20 parts.	do.	3	82	2	55	25	0	0	0	0	0	0	0	0	0	100.00
Derris powder, 8 ounces; soap, 4 ounces; water, 1 gallon.	Wash on back, 2 applications.	9	11	0	0	7	0	0	0	0	0	0	0	0	4	100.00
Do.	Wash on back, 1 application.	18	109	1	65	134	0	0	0	0	0	1	10	65.66		
Derris powder, 12 ounces; soap, 4 ounces; water, 1 gallon.	Wash on back, 2 applications.	8	21	0	1	19	0	0	0	0	0	0	0	0	1	100.00
Do.	Wash on back, 1 application.	26	191	1	51	137	0	0	2	0	0	0	0	0	0	98.95
Derris powder, 16 ounces; soap, 4 ounces; water, 1 gallon.	do.	55	503	1	495	17	0	0	0	0	0	0	0	1	98.61	
Do.	Wash on back, 2 applications; first application, 4 ounces of derris.	5	92	1	89	0	0	0	0	0	0	0	0	3	100.00	

¹ Includes all stages. Mostly fifth-stage larvae, but all stages not determined.

TABLE 11.—Treatment of *Hypoderma lineatum* in the backs of cattle, Dallas, Tex., 1918-1924—Continued

Material and strength	How applied	Number of cows treated	Number of grubs treated	Number of grubs killed			Number of grubs not killed			Number of grubs doubtful			Number of grubs gone			Percentage killed based on dead and alive	
				Stage			Stage			Stage			Stage				
				3	4	5	3	4	5	3	4	5	3	4	5		
Derris powder, 12 ounces; water, 1 gallon.	Wash on back, 1 application.	11	78		1	47		1	31		0	0	0	0	0	0	60.26
Gasoline	Injected with syringe	9	34	0	10	14	0	0	1	0	1	8	0	0	0	0	96.00
Do	Injected with oil can	19	91	0	6	34	0	2	17	0	0	6	0	0	26	0	67.80
Hellebore, dry	Dusted into hole	1	20	0	3	8	0	1	4	0	1	3	0	0	0	0	68.75
Iodine, tincture, U. S. P., 25 per cent.	Injected with syringe	1	12	0	0	5	0	0	7	0	0	0	0	0	0	0	41.66
Iodine, tincture, U. S. P., 100 per cent.	do	68	437	0	0	204	0	0	111	0	27	95	0	0	0	0	64.76
Iodoform, 1 part; petrolatum, 10 parts.	Pressed into hole	57	255	0	12	197	0	0	12	0	0	2	0	0	32	0	94.57
Iodoform, 1 part; petrolatum, 5 parts.	do	88	480		1	410		1	37		0	0	1		1	32	91.72
Do	Rubbed on bumps	12	21		1	12		1	6		0	0	0		1	3	66.66
Iodoform, 1 part; petrolatum, 3 parts.	Pressed into holes	10	67	0	1	42	0	0	0	0	0	0	0	0	0	24	100.00
Iodoform, 1 part; petrolatum, 1 part.	do	41	223	1	8	179	0	3	16	0	1	4	0	0	11	90.82	
Kerosene emulsion, 22.2 per cent oil.	Wash on back, 2 applications.	13	41	0	2	8	0	1	30	0	0	0	0	0	0	0	24.39
Kerosene, 25 per cent; lard, 75 per cent.	Pressed into holes	9	60	0	1	11	0	0	17	0	0	31	0	0	0	0	41.38
Kerosene	Injected with oil can	10	67	0	0	32	0	1	14	0	0	3	0	0	17	68.09	
Lime-sulfur solution, 1.92 per cent active ingredients.	Wash on back, 2 applications 24 hours apart.	22	147		1	144		1	100		1	2		0	0	1	30.56
Lubricating-oil emulsion	Oil can, 1 application	6	59	1	5	6	0	17	27	0	0	1	0	0	2	21	43
Nicotine sulfate, 0.08 per cent; soap, 2 ounces per gallon.	Wash on back, 2 applications 36 hours apart.	28	73	0	0	14	0	1	29	0	0	0	0	0	0	29	31.82
Nicotine sulfate, 0.1 per cent; soap, 2 ounces per gallon.	Wash on back 2 applications 48 hours apart.	14	52	0	0	5	0	1	28	0	0	0	0	0	18	14	71
Nicotine sulfate, 0.4 per cent nicotine.	Injected with syringe	2	10	0	3	1	0	0	4	0	0	0	0	0	2	50	00
Nicotine dust, 2 per cent.	Dusted into hole	27	77	0	0	74	0	0	0	0	0	0	0	0	3	100	00
Nicotine, free, 0.2 per cent.	Injected with syringe, 1 application.	14	88	0	7	15	1	11	42	0	0	2	0	0	10	28	95
Nicotine, free, 0.52 per cent.	do	18	164	0	17	63	0	23	42	0	0	1	0	0	18	55	17
Nicotine, free, 0.52 per cent; soap.	do	14	100	0	17	54	0	1	12	0	0	1	0	0	15	84	52
Nitrobenzene	Injected with syringe	20	68	0	16	34	0	1	7	0	0	1	0	0	9	86	21
No chemical used	Stiff brush, hard rub.	2	10	0	0	1	0	0	6	0	0	0	0	0	3	14	29
Paraffin oil	Injected with syringe	18	88	0	0	55	0	33	0	0	0	0	0	0	0	62	50
Petroleum (fuel) oil	do	8	30	0	0	5	0	0	9	0	1	15	0	0	0	35	71
Pine-tar oil, crude, ¾ per cent phenol.	Injected with oil can, 1 application.	13	163	3	125	18	0	7	6	0	2	0	0	0	2	91	82
Pine-tar oil, refined	do	20	162	0	34	55	0	42	0	0	0	0	0	0	31	67	94
Pine tar	Rubbed on bumps	6	35	0	0	13	0	8	0	0	14	0	0	0	0	61	90
Pine-tar oil, commercial, 2 parts; furfural, 1 part; 90 per cent benzol, 1 part.	Dropped in holes	3	14	0	2	6	0	0	6	0	0	0	0	0	0	57	14
Pine tar, 1 part; paraffin oil, 1 part.	Injected with syringe	4	14	0	2	6	0	0	0	0	1	5	0	0	0	100	00
Potassium permanganate, 25 per cent of a saturated solution.	do	4	4	0	0	4	0	0	0	0	0	0	0	0	0	100	00
Potassium permanganate, 50 per cent of a saturated solution.	do	1	6	0	0	5	0	0	1	0	0	0	0	0	0	83	33
Potassium permanganate, saturated solution.	do	24	146	0	5	101	0	0	34	0	0	6	0	0	0	75	71
Pyrethrum flowers, 2 pounds; grain alcohol, 96 per cent, 1 gallon. ²	Injected with oil can	21	75	1	30	12	0	4	24	0	0	1	0	0	3	60	56
Pyrethrum flowers, 2 pounds; alcohol (denatured, formula 5); 1 gallon. ²	do	2	19	0	14	5	0	0	0	0	0	0	0	0	0	100	00
Pyrethrum flowers, 2 pounds; alcohol (grain, denatured, formula 5), 1 gallon. ²	Wash on back	21	111	0	11	41	0	1	39	0	0	4	0	0	15	56	52
Pyrethrum flowers, 2 pounds; benzol (90 per cent), 1 gallon. ²	Injected with oil can	11	126	1	74	49	0	0	1	0	0	1	0	0	0	99	20

¹ Includes all stages. Mostly fifth-stage larvæ, but all stages not determined.² Open pyrethrum flowers. Macerated for 24 hours and strained.

TABLE 11.—Treatment of *Hypoderma lineatum* in the backs of cattle, Dallas, Tex., 1918-1924—Continued

Material and strength	How applied	Number of cows treated	Number of grubs treated			Number of grubs killed			Number of grubs not killed			Number of grubs doubtful			Number of grubs gone			Percentage killed based on dead and alive
			Stage			Stage			Stage			Stage						
3	4	5	3	4	5	3	4	5	3	4	5	3	4	5				
Pyrethrum flowers, 2 pounds; carbon tetrachloride, 1 gallon. ²	Injected with oil can.....	24	107	8	63	35	0	0	0	0	0	0	0	0	100.00			
Pyrethrum flowers, 2 pounds; kerosene, 1 gallon. ²	do.....	20	173	6	110	47	0	2	8	0	0	0	0	0	94.22			
Pyrethrum-kerosene extract, ² emulsified with soap and water, 0.44 pound per gallon of emulsion containing 0.22 per cent oil.	Wash on back, 1 application.	12	91	0	6	9	0	9	58	0	0	0	0	0	18.29			
Pyrethrum powder (open flowers), 1 part; petrolatum, 2 parts.	Pressed into holes.....	22	100	0	8	76	0	0	0	0	0	0	1	0	100.00			
Pyrethrum powder (open flowers), 1 pound; soap, 4 ounces; water, 1 gallon.	Wash on back, 1 application.	8	87	0	2	9	0	2	57	0	0	0	0	0	15.71			
Pyrethrum powder (open flowers).....	Dusted into holes.....	1	22	0	2	2	0	1	7	0	3	7	0	0	33.33			
Silver nitrate, 5 per cent.....	Injected with syringe.....	4	30	0	0	15	0	0	0	0	15	0	0	0	100.00			
Silver nitrate, saturated solution.....	do.....	1	20	0	0	20	0	0	0	0	0	0	0	0	100.00			
Solvol, 10 per cent.....	do.....	2	13	0	0	12	0	0	1	0	0	0	0	0	92.31			
Soap, 4 ounces; water, 1 gallon.....	Wash on back.....	1	21	0	0	0	0	19	0	0	0	0	0	3	00.00			
Sodium chloride, saturated solution.....	do.....	3	21	0	0	3	0	0	18	0	0	0	0	0	14.29			
Sodium chloride, dry.....	Dusted into holes.....	16	91	0	0	14	0	2	45	0	0	30	0	0	22.95			
Sodium fluoride, 75 per cent, saturated solution.....	Injected with syringe.....	6	22	0	1	9	0	0	6	0	3	3	0	0	62.50			
Sodium fluoride, dry.....	Dusted into holes.....	1	3	0	0	0	0	1	1	0	0	1	0	0	00.00			
Sodium hypochlorite, 1 ounce; water, 16 ounces.....	Injected with oil can.....	6	46	1	1	8	1	2	33	0	0	0	0	0	21.74			
Sulfur, 1 part; petrolatum, 2 parts.....	Pressed into holes.....	15	45	1	16	8	0	10	10	0	0	0	0	0	55.55			
Tobacco dust, fine, 1.08 per cent nicotine.	Dusted into holes.....	36	146	0	3	105	0	1	18	0	0	0	0	0	85.04			
Tobacco dust, 1 part; petrolatum, 2 parts; 0.33 per cent nicotine.	Pressed into holes.....	23	231	0	60	147	0	14	4	0	0	0	0	0	92.00			
Tobacco-dust infusion No. 1 ³	Injected with oil can.....	12	97	0	22	15	0	19	29	0	0	1	0	0	43.53			
Tobacco-dust infusion No. 2 ³	Wash, 2 applications on successive days.	4	27	0	17	10	0	19	0	0	0	0	0	1	65.38			
Tobacco-dust infusion No. 3 ³	do.....	5	87	0	9	57	0	4	16	0	0	0	0	1	76.74			
Tobacco-dust infusion No. 4 ³	Wash, 1 application.....	5	77	0	4	27	0	10	33	0	0	0	0	3	41.89			
Tobacco-dust infusion No. 5, ³ 0.22 per cent nicotine.	Wash, 4 applications; 2 on successive days; 2 weeks apart.	39	360	0	128	103	0	32	69	0	4	6	0	0	69.58			
Tobacco-dust infusion No. 6, ³ 0.22 per cent nicotine.	Wash, 2 applications 2 weeks apart.	2	39	275	0	90	56	0	16	77	0	8	5	0	61.09			
Tobacco-dust infusion No. 7, ³ 0.22 to 0.32 per cent nicotine.	Wash, 5 applications 1 week apart.	44	336	0	134	115	0	13	44	0	4	3	0	0	81.37			
Tobacco-dust infusion No. 8, ³ 0.52 per cent nicotine.	Wash, 1 application.....	18	101	0	6	34	0	8	40	0	0	0	0	0	45.45			
Tobacco-dust infusion No. 9, ³ 0.51 to 0.54 per cent nicotine.	Wash, 3 applications, 1, then 2 one week later.	21	95	0	5	53	0	2	8	0	0	0	0	0	85.29			
Turpentine spirits, undiluted.....	Injected with syringe.....	7	78	0	0	60	0	0	4	0	0	14	0	0	93.75			
Do.....	Injected with oil can.....	50	213	0	2	80	0	2	54	0	1	2	0	0	59.42			
Disinfectant (phenol, boracic acid, alum).	Injected with syringe.....	3	14	0	0	9	0	0	0	0	0	5	0	0	100.00			

³ These tobacco infusions, Nos. 1 to 9, were made with ingredients in the following proportions: No. 1, 4 pounds of tobacco dust, sufficient water to make 1 gallon; No. 2, 1 pound of English tobacco dust, 4 ounces of stone lime, sufficient water to make 1 pint; No. 3, for first application, 1 pound of tobacco dust, 1 ounce of lime, sufficient water to make 1 gallon; for second application, three-fourths pound of tobacco dust, 1 ounce of lime, sufficient water to make 1 gallon; Nos. 4, 5, 6, and 7, 4 pounds of tobacco dust, 1 pound of lime, sufficient water to make 1 gallon; Nos. 8 and 9, 8 pounds of tobacco dust, 4 pounds of lime, sufficient water to make 1 gallon.

TABLE 12.—Treatment of *Hypoderma lineatum* and *H. bovis* in the backs of cattle, Orange County, N. Y., 1922

Chemicals used	How applied	Number of cows treated	Number of grubs treated					Number of grubs not killed					Number of grubs doubtful					Number of grubs gone					Percentage killed based on dead and alive	Species
			Stage					Stage					Stage					Stage						
			3	4	5			3	4	5			3	4	5			3	4	5				
Derris, 1 part; petrolatum, 10 parts.	Rubbed in, 1 application.	4	64		164			0	0	0			0	0	0			0	0	0			100.00	<i>Hypoderma bovis</i> and <i>H. lineatum</i> . Do.
Derris, 1 pound; soap, 4 ounces; water, 1 gallon.	Wash on back, 1 application.	9	91		163			1	21				1	7				0	0	0			75.00	
Derris, 1 ounce; water, 300 ounces; soap, 5½ ounces.	do.	2	43	0	0	0		0	0	43	0		0	0	0			0	0	0			00.00	<i>H. bovis</i> .
Derris extract, 1 part; water, 100 parts; soap, 1 part.	do.	6	23	0	0	2		0	17	0			0	0	0			1	4				10.53	Do.
Iodoform, 1 part; petrolatum, 5 parts	Rubbed in, 1 application	19	206		163			1	42				0	0	0			1	1				79.51	<i>H. bovis</i> and <i>H. lineatum</i> . <i>H. bovis</i> .
Nicotine (free), 0.1 per cent solution.	Wash on back, 1 application.	6	100		114			1	69				1	2				1	15				16.87	
Tobacco dust, dry	Rubbed in, 1 application.	4	67		13			1	60				1	1				1	3				4.76	Do.
Tobacco infusion: Tobacco dust, 4 pounds; lime, 1 pound; water, 1 gallon.	Wash on back, 2 applications 24 hours apart.	3	115		119			1	56				1	21				1	19				25.33	Do.
Sodium hypochlorite, 2 ounces; water, 16 ounces.	do.	1	5	0	0	2		0	0	3	0		0	0	0			0	0	0			40.00	Do.

¹ Includes all stages. Mostly fifth-stage larvæ, but all stages not determined.

Several different methods were considered of computing the percentage of the grubs destroyed by the various materials, but it was finally decided to make this computation on the basis of the number of grubs found alive or dead at the time of examination. This gives considerable advantage to those materials which had low killing power, as in many cases the mature larvæ which were uninjured would leave the host before the results were checked. Furthermore, in the case of those substances which were very toxic, especially the ointments, many of those grubs recorded as gone were no doubt killed or were so weakened as never to produce adults. Those recorded as doubtful were, for the most part, larvæ which were extracted four or five days after treatment. In the case of some of the substances it was found difficult to determine for certain in every case whether the grubs were dead or alive when observations upon them were made so soon after treatment. From six to eight days proved to be the most satisfactory interval between treatment and determination of result.

In general it may be stated that in the case of those materials which gave a very high percentage of mortality relatively few grubs were gone at the time of examination. Some of the ointments may be noted as exceptions to this, as they were found to facilitate the emergence of the grubs from the skin even though the grubs were dead.

Attention is especially directed to the results secured by the use of the following materials: Benzol and carbon tetrachloride when in-

jected into the cysts; derris used in dry form, as an ointment with petrolatum, or in suspension in water when injected into the cysts, or applied as a wash (111); iodoform and petrolatum, also pyrethrum and petrolatum, when applied as an ointment; and very fine tobacco dust and nicotine dust used in powder form.

The results of the writers' work seem to indicate rather clearly that the percentage of mortality is not so high in the case of *H. bovis* as with *H. lineatum*.

The treatment of cattle in practice requires the application of a method which will be as effective as possible under adverse conditions. When treatments are given by the livestock owners themselves, washes applied to the entire back of the animal are probably the most dependable, in that the inexperienced operator is more likely to treat all of the grubs than if the latter have to be found individually. On the other hand, there may be some objection to the use of washes on the entire back of the animal under certain adverse weather conditions. An objection to the use of the syringe is that the instrument is an item of expense and may be broken even if carefully handled. This tends to commend the oil can if the grubs are to be injected individually. In the writers' experience they have found that an oil can with a comparatively slender curved point is the most convenient to use. If the aperture in the spout is not too large the spout can be utilized to advantage in finding the grub hole. One advantage in the use of an ointment such as iodoform-petrolatum is that the operator can easily recognize which grubs have been treated. The use of powders is favored by those who do not wish to wet the animals during the winter, but some objection might be had to them on account of the possibility of the dust getting into the buckets during milking. With certain washes, however, the dust is left in the hair after the animal has dried. A careful application of dust to the backs of cattle is almost as certain to reach all grubs as the use of a wash.

Tobacco infusion has been advocated for the destruction of grubs in the backs of cattle by Carpenter, Phibbs, and Slattery (19). Although results of the writers' preliminary tests with similar infusions were not satisfactory, they continued their experiments after receiving Carpenter's favorable reports. In his early publications he gave no idea of the strength of the decoctions he used, and it appears that he must have employed infusions with a higher percentage of nicotine than the writers were able to obtain from American tobacco dusts by using his formula. When, however, tobacco dust from the same source as that employed by Carpenter (see Table 11, tobacco infusion No. 2) was used, the mortality obtained (65.38 per cent) was not nearly so high as reported by Carpenter. With most of American tobacco dusts, which run from 1 to 1½ per cent nicotine, great difficulty was found in obtaining an infusion containing 0.5 per cent of nicotine. In order to get such a percentage the amount of tobacco dust advised in Carpenter's formula was doubled, being 8 pounds of tobacco dust, 4 pounds of stone lime, and 1 gallon of water. In preparing this the lime was first slaked in the water, and then the tobacco dust was stirred in and allowed to stand about 24 hours. The mass was then placed in a sack and pressure

applied at times with two boards hinged at one end. From 1 gallon of water usually not more than 3 pints of infusion was obtained. Serious objections to the use of this decoction are the labor involved in preparing it and the great variability in the strength of the infusion obtained. These objections would cause the investigator or stockman to turn to the standardized solutions of free nicotine or nicotine sulfate, but the results obtained with these substances when used at strengths which would not endanger the host were unsatisfactory. Nicotine sulfate at a strength of 0.4 per cent when injected into the cysts of the grubs gave a mortality of only 50 per cent, and free nicotine at a strength of 0.52 per cent with soap added resulted in a mortality of 84 per cent. These strengths are greater than would be advisable for use as general washes on the backs of cattle.

The toxicity, to larvæ in different stages, of materials applied to the backs of cattle is a point of importance. It is necessary, of course, to kill a high percentage of all stages of larvæ present at the time of treatment, but for several reasons it is desirable that treatment be made with a view of destroying the grubs while small. To gain some information on this question a study of the percentage of mortality among the different stages was made. For comparison the percentages of mortality among the grubs in the fourth and fifth stages treated with fairly effective larvicides were compared. The materials used were grouped according to method of treatment. These groups and the mortality of the larvæ in each were as follows: Cysts injected with syringe or oil can, fourth stage 91.01 per cent, fifth stage 81.21 per cent; ointments applied to the opening in the skin, fourth stage 84.34 per cent, fifth stage 93.32 per cent; dusts applied to the openings in the skin, fourth stage 83.33 per cent, fifth stage 88.05 per cent; washes applied to backs of cattle, fourth stage 90.29 per cent, fifth stage 68.77 per cent. These figures should not be taken to indicate the relative merits of the different methods of treatment. They are of value, however, because they clearly show that the ointments and powders are relatively more effective against the larvæ of the fifth stage than against those of the fourth, probably owing to the larger apertures in the skin, which permit the materials more readily to gain access to the larvæ; but, on the other hand, that the percentage of mortality is higher in larvæ of the fourth stage than in those of the fifth when the insecticides are injected into the cysts or applied as washes to the backs of the cattle. It appears that the younger stages are somewhat more easily killed than the fifth-stage larvæ when they are actually brought into contact with the insecticide. Exact observations on the mortality among third-stage larvæ have not been made in a sufficient number of specimens to form a reliable basis for conclusions, but for the purpose of comparing the relative susceptibility of the three stages to various treatments, it may be said that the mortality runs about 92 per cent in the third stage, 89 per cent in the fourth stage, and 83 per cent in the fifth stage.

EXTRACTION OF GRUBS BY HAND

It is the common belief that the cattle grubs must be fairly well matured before they can be successfully removed by hand. The expression is often heard, "the grubs are not yet ripe."

In the writers' experience they have found that grubs may be extracted at any time during the course of their development in the backs of the cattle. They have found that, by removing the small scabs which usually develop around the apertures cut by the young or third-stage larvæ, they can be pressed out with great ease. There seems to be a period in the fourth stage during which extraction is more difficult. By using care, however, practically every grub can be removed by hand. (Fig. 36.)



FIG. 36.—Extracting *Hypoderma* larva from cow by pressing down around cyst opening

There is a very marked difference in the ease with which grubs may be extracted from the backs of cattle of different breeds. In the case of the island breeds the skin appears more flexible and elastic, and extraction is comparatively easy. Very often with the Holstein-Friesian and certain beef breeds it is almost impossible to squeeze the grubs out by hand. The condition of flesh of the host also has a considerable effect on the ease of extraction. Very poor or extremely fat cattle are more difficult to treat than those in fair condition.

The method of procedure in extracting grubs may be modified to suit the individual and also the character of the skin of the host under treatment. Inexperienced people often find extraction extremely difficult; but those who have considerable experience are able to remove the grubs with comparative ease, and they seldom break

the cyst and allow the larva to escape. Certain writers have advocated the application of salt water or soapy water to the backs of cattle before extraction is begun. It is probable in the case of cattle with elastic skins that a weak saline solution applied to the backs some time before extraction is undertaken will aid the work. In the present writers' experience, however, washes have not been found materially to facilitate extraction. (See further discussion under "Cost of treatment or extraction of grubs," p. 106.)

MECHANICAL EXTRACTION OF GRUBS

One often hears of the old-fashioned method of placing the mouth of a heated bottle over the aperture of the grub. Some larvæ may be extracted by this method, but it is extremely slow. It suggests, however, the possibility of utilizing suction and pressure in extraction work. For several years the writers have given considerable attention to the question of developing an implement for removing the grubs from the backs of cattle by suction. One of the principal difficulties encountered is in obtaining an airtight cup to fit over the warble and to generate, without unduly complicated and expensive apparatus, a sufficient vacuum to suck the grubs out of the cysts. Brodersen (11), a veterinarian in Denmark, has devised and patented a small suction pump operated by hand which he considers a success for the removal of grubs. The principle employed is a combination of pressure and suction. The end of the pump barrel is fitted with a rubber cup which is applied to the back of the animal over the grub hole. This is pressed down against the animal while the plunger is being pulled out, thus creating a partial vacuum. Doctor Brodersen has very kindly furnished the writers with one of these instruments, but in their experiments it has not worked well, especially on animals with inelastic skins. In certain instances, even though tremendous pressure was applied and the plunger raised a great many times, the grubs could not be pulled out of their cysts. Before receiving Brodersen's extractor, the writers had developed a similar instrument made from an old automobile-tire pump (fig. 37). This, probably owing to a larger barrel capacity, gave even better results than the imported extractor. There is certainly some advantage in using an instrument of this kind if it can be developed to a point where a large percentage of the grubs can be removed without consuming too much time. It would be less trying on the fingers than hand extraction and the operator would not have the disagreeable experience, which often comes from squeezing the grubs out by hand, of having pus, or the contents of the grub, squirted into the face. Furthermore, it is probable that the chance of breaking the cysts or bruising the tissues would be less than might result from hand extraction, especially by an inexperienced operator.

The use of forceps to assist in the extraction of larvæ naturally comes to mind. The writers have investigated the possibility of using various types of forceps in this work. One of the principal difficulties is in obtaining a pair of forceps with sufficiently fine points to enter the small holes in the hide and at the same time with enough strength to extract the larvæ and not get out of order. One of the most successful forms of forceps tried is the alligator-jaw

type (fig. 38). These permit one to place the tips well into the hole and then to open them and secure a firm hold on the grub. Another type which has been found very successful is a simple forceps with stout shanks and provided at the tip with minute mouse-teeth. These, however, often puncture the grub, which might be considered objectionable by some.

The enlargement of the grub holes in the hide by cutting, is a method suggested by some, especially by veterinarians. It has been found that in most cases this practice causes the host too much discomfort. There is also the possibility of cutting through the cyst, if the incision is made too deeply, and thus allowing some of the foreign matter to enter the tissues of the host.

Certain stockmen have for years practiced the plan of puncturing the grub before attempting to extract it. This led the writers to



FIG. 37.—Removing *Hypoderma* larvæ from back of cow by means of suction pump of the Brodersen type

make a series of tests of this method. One of the procedures followed was to press firmly around the grub, thus bringing it up to the aperture in the skin, and then to clip the posterior end with a pair of fine-pointed scissors. A small amount of pressure applied to the cyst will expel the contents of the larva, after which the skin of the grub may be easily extracted by pressure, or better, with a pair of forceps. In certain instances grubs punctured in the way described were left in the host. In a short time it was found that the skins of most of these grubs had protruded some distance from the holes in the skin, thus enabling one to remove them easily with the fingers.

EFFECT ON HOST OF DESTRUCTION AND EXTRACTION OF GRUBS

Despite the very general practice of extracting grubs by hand which has been employed for many years, not until recently have

any definite ill effects been attributed to this method. Brodersen (10), working in Denmark, reports his observations upon a semiacute malady which he terms "Rosenfeber." He records several cases in which he has seen the sick cows very soon after the grubs had been squeezed out. The description he gives of the sickness indicates clearly that it is of an anaphylactic nature similar to that described by Hadwen and Bruce (38), Jensen (49), and Van Es and Schalk (109) in cases where they injected the juice of larvæ into animals sensitized by natural infestations. Brodersen's cases were acute but not serious. Apparently the general depression, rapid pulse, and puslike secretion from the mucous membranes completely subsided within a few hours. In the cases cited it appears that the grubs were squeezed out by men hired for the purpose and apparently the work was done in a very crude way. The experience, however, directs attention to the danger of handling cattle roughly during the extraction process and further emphasizes the need of a proper understanding of the best method of removing the grubs. It should be noted also that in cases in the writer's experience in which the grubs have been removed from large numbers of cattle, some of them very heavily infested, no instance in which any ill effects whatsoever were noticeable has ever been observed. The principal danger seems to lie in the improper application of pressure around the grub, which causes the cyst to break and the grub, after being crushed, to be forced back into the connective tissue.

To lessen the danger of anaphylactic shock to cattle following hand extraction of grubs, Hadwen (37) has advised that the back of the animal be washed off with cold water. In very valuable animals and show herds, it is suggested that the warble cysts be washed out with a hypodermic syringe or oil can, using a normal saline solution or a 2 per cent carbolic wash.

Aside from the anaphylactic reaction mentioned above it is claimed by some that there is occasional formation of pus abscesses in the subcutaneous tissue following extraction. The writers' observations indicate, however, that with even moderate care in hand extraction the chance of pus formation in the backs of stock is lessened rather than increased by removing the grubs. Great numbers of cases have been encountered in which cows had developed large abscesses without having been treated for grubs, usually because of the closing of the orifice of the grub cyst before the grub reaches maturity. In most cases this results in the death of the insect. Such abscesses are always greatly relieved by discharging them as soon as they are observed.

Realizing the fact that the leaving of foreign bodies in a host is not good surgical practice, the writers were at first rather skeptical about the advisability of destroying the grubs in the backs

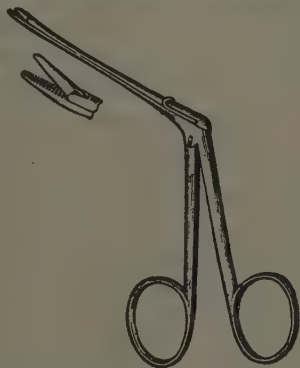


FIG. 38.—Alligator forceps, a type well adapted for use in extracting grubs from the backs of cattle

of cattle by the application of insecticides. The difficulty of removing the grubs from certain breeds, however, led them to give very serious consideration to this method of treatment. As a result of rather extended experiments and practical demonstrations of this method, it became evident that no ill effects were visible in the host. It is true that certain materials may be used in the destruction of the grubs which are detrimental to the host, as, for instance, copper sulfate. In the writers' tests this material gave decidedly bad local effects. Abscesses were developed in a considerable percentage of the cysts treated. On the other hand, with many of the most effective larvicides tried, pus formation in the cysts was checked and the size of the lump caused by the grub was rapidly reduced.

With some treatments, notably those with carbon tetrachloride, and with derris in various forms, the exit holes of the grubs were observed to close rather rapidly and there was little tendency for the host to expel the insect. In most instances the grubs were found to disintegrate rather rapidly under such conditions, especially if they were not in the late stages of development. At times some of the grubs, especially in the late fifth stage, were found to rise in the aperture in the skin and the posterior segments to harden, thus retarding the closing of the hole in the skin.

When the grubs are not further developed than the early part of the fifth stage, they are promptly absorbed after being killed by substances applied to the back of the host. After the skin and spines have become thoroughly chitinized their elimination by the host is more difficult. Some collapse and work out or are licked out of the skin. Most of them are reduced in bulk by absorption and the skin heals up smoothly over them. A considerable percentage of these mature grubs may remain in the skin for several months. This shows the advisability of applying treatments while the grubs are young; furthermore, at this time the holes in the hides are much smaller and heal up more quickly.

When ointments such as iodoform, derris, or pyrethrum and petrolatum are used, the writers have found that a considerable percentage of the grubs are expelled from the cysts after their death. Some of them are found completely emerged from the skin of the host two days after treatment and they continue to be thrown off for about two weeks. Some project slightly from the skin and may remain so for weeks if not mechanically removed. The percentage of grubs which are expelled after treatment varies widely, apparently differing with the character of the skin of the host.

In order to determine the effect on the host and the rapidity of healing of the grub holes, some special observations were made on herds (1) where grubs left the hosts normally, (2) where the larvæ were punctured and pulled out, (3) where they were extracted by hand, and (4) where various materials were applied to the backs of the cattle. The rapidity of healing of the grub holes was found to vary much in different animals, both when the grubs emerged normally and when they were extracted or destroyed *in situ*. It was found that the time required for healing of holes where the grubs emerged normally ranged from about 13 to 76 days. The scars from the skin injury often persist for several months. The presence of foreign material in the form of a plug in

the grub aperture often retards healing. This may contain the exuviae of the larvæ, but usually it seems to be composed of dried excretions from the cyst. As the opening heals about this tough material there often remains a pit containing a minute hole which can be located with a pointed instrument.

Observations have been carried on to determine the rapidity of healing of grub holes in the skin when the grubs are killed by the application of insecticides or are extracted by hand. It has been observed that where grubs are squeezed out, or even drop normally, the old cyst and other material left within it require several weeks for absorption. Grubs were extracted on one side of the backs of cattle and on the corresponding side they were killed with insecticides. Two weeks later these animals were slaughtered and examined. The condition of the connective tissue around the grub cysts was practically identical on both sides. When the skin was removed no discolored or infiltrated tissue was left on the carcass, but the former position of the grubs could be located on the under side of the hide. The holes in the hide had healed to about the same degree with the exception of a few cases in which portions of the bodies of the dead larvæ were in the grub openings, thus preventing the closing of the apertures.

In several herds in which insecticides were administered to the backs of the cattle, a number of subsequent examinations were made to determine the general condition of the infested areas and the rapidity with which the skin healed. In most of these herds the grubs were not treated until many of them were nearly mature. Seventy-seven days following the treatment it was found that between 42 and 62 per cent of the grub holes had healed, and the fact that the animals had been infested with larvæ could not then be determined by touch. One hundred and twelve days following treatment 75 per cent of the grub holes were completely healed and smooth. At this time only 2 per cent remained open and in no case was more than a very slight quantity of pus present. In one herd treated with benzol it was found that the healing was less advanced at the end of 77 days. Only 30 per cent of the grub holes were healed and smooth, and 48 per cent of the holes were still open. The presence of the grubs was apparent in 25 per cent of the cysts. In all cases, however, the warbles were distinctly reduced in size.

Since in certain animals extraction is greatly facilitated by puncturing the grubs and squeezing out their contents before removing the grub skin, the writers have treated over 200 head in this way. In no instance did the condition of the lesions and the rapidity of the healing of the holes in the skin show any difference from those in cases in which the grubs were extracted by squeezing. In a number of cattle the grubs were punctured and left in the cyst after the body contents had been pressed out. No ill effects were observed, but healing of some of the holes in the skin was retarded, owing to the hardening in them of the skins of the grubs. One animal treated in this way had 60 well-developed grubs in its back. Six days after the puncturing, about 10 of the grubs were projecting from the skin. These were shrunk and hardened, and seven of these were pulled out. There was no more pus in any of the cysts than would occur with living larvæ. Twelve days later six

projecting grubs were pulled out; the cysts under these were small and the animal had improved noticeably in condition of flesh. At this time more than one-half of the holes were healed. When the grubs are punctured before they are extracted the cattle are worried much less than when extraction by the usual method is practiced. Schöttler (87) states that in Germany a crochet needle has been used for puncturing and extracting grubs, but that this method had been found to be undesirable because the juice from the grubs may cause nettle fever.

COST OF TREATMENT OR EXTRACTION OF GRUBS

To gain information on the expense of treating cattle for grubs, records were kept on the time required in applying the different treatments, the quantity of the material used, and its cost.

It was found that for cattle of the island breeds hand extraction was the most economical. The time consumed in extraction varied considerably with the breed and with the local conditions under which the work was done, as well as with the experience of the operator. The rate of extraction per hour ranged from 38 grubs in Holsteins to 191 in a dairy herd of mixed breeds. It appears that with the average herd of Jerseys or mixed breeds, not Holsteins, the grubs can be extracted carefully and thoroughly at the rate of about 125 per hour. Naturally the degree of infestation affects the rate, as in very light infestations much time is occupied in going from one animal to another and in very heavy infestations more care is necessary to avoid missing some grubs.

In tests in which the backs of the cattle were thoroughly moistened with soap solution the average number of larvæ extracted per hour was 119, and where normal salt solution was applied prior to the extraction the grubs were removed at the rate of 100 per hour. These tests therefore seem to indicate that the wetting of the backs of the cattle in the case of island or mixed breeds, not Holsteins, tends to retard the rate of extraction.

In tests of the method of extracting the grubs after puncturing them and expelling the contents, the average number of grubs removed per hour was slightly over 88. This work was done without special forceps, which if used would have hastened the work. Although this rate of extraction is considerably slower than that of the hand extraction in Jersey or mixed herds it is decidedly more rapid than hand extraction in Holsteins.

The rate of treatment when injecting the cysts with a hypodermic syringe ran about 170 grubs per hour. The time consumed in injecting the material by means of an oil can varied considerably, ranging from 74 to 240 grubs per hour. The very slow record mentioned was probably due to the fact that a large number of the grubs had dropped, and it was necessary to examine each cyst to determine if the larva was still present. Under good conditions in a dairy it is thought that by the oil-can injection method 225 grubs per hour might be readily treated.

The application of such general treatments as dusts and washes is considerably more rapid than the individual treatment of grubs. The thoroughness with which either of these methods must be carried out, however, causes more time to be consumed in the treat-

ment than would be supposed. On an average it required an hour to treat about 98 grubs by the application of ointments, such as iodoform-petrolatum to cysts in the backs of cattle. Undoubtedly this work could be done much more rapidly in herds showing a fairly heavy infestation.

The cost of materials and equipment should be considered, especially if large herds are to be treated. The fact that no instruments or materials are needed for the ordinary hand extraction commends that method. With the use of ointments, powders, and washes practically no equipment is required. The cost of forceps or scissors for the puncturing and pulling method of extraction is not great, but this method requires rather more care and a higher degree of training for the work than is necessary for using the oil-can injection method or for applying washes and powders.

The cost of the chemicals used varies considerably with the material, and there is also considerable difference between the wholesale and retail prices of each. Iodoform-petrolatum ointment costs about $8\frac{1}{4}$ cents per ounce at the usual wholesale price. The retail price is about 15 cents per ounce. An ounce will treat between 125 and 200 grubs, thus making the retail cost of the ointment about 12 cents per 100 grubs. Pyrethrum ointment is much cheaper, as it costs about 5 cents per 100 grubs. The only objection to this ointment is that the pyrethrum powder must be fresh to be potent.

With such materials as carbon tetrachloride and benzol, it was found that a pound of either would treat about 500 warbles. Since these materials are comparatively inexpensive the cost is extremely low.

As yet derris is not available on the open market in this country, but it is probable that it will retail at approximately \$1 per pound. Tobacco dusts of all grades are very much cheaper, but they do not appear to be equally effective in any strength, and furthermore their strength as well as mechanical make-up varies considerably. It is probable that if further tests prove that very fine tobacco dust with a fairly high percentage of nicotine is as effective as the writers' preliminary experiments indicate, this material may be standardized for this purpose.

CONTROL THROUGH INDIVIDUAL EFFORT

The results of control measures applied by an individual cattle owner when he is more or less closely surrounded by livestock are likely to be disappointing. Three tests have been made by the writers in which the grubs have been destroyed rather systematically for periods of from two to four years. It is true that all grubs were not destroyed each year, but the work was probably done as thoroughly as it would have been if left to the cattle owners. The pastures where the treated cattle ranged were in close proximity to others in which untreated stock were kept. In none of these tests was a striking reduction observed in the number of grubs during the year following.

The most thorough work along this line was done on the dairy and breeding farm of J. T. Orr, near Dallas, Tex. From 45 to 100 head of cattle were carried on this place. During the grub season of 1920-21 the cattle were examined and grubs destroyed only once, on January 29. The average number of grubs per head then was

5.13. In 1921-22 the cattle were all examined and grubs extracted on December 16 and January 17, the average per head being 3.55. In 1922-23 the grubs were all extracted on November 28, December 28, January 29, and March 21, the average per head for the year being 11.30. During 1923-24 the cattle were gone over four times and an average for the year of 7.5 grubs per animal was found. During the last three seasons the work was done very thoroughly yet it appears that enough flies entered the pasture from adjoining farms to keep up the infestation. It is thought that this is a rather peculiar case, however, on account of certain local conditions.

Duncan, Hewitt, and Jardine (28) have reported a similar experience on a farm in Ireland. The average number of grubs was materially lowered after the first year's destruction, but for several succeeding years it remained rather constant, though relatively low.

The writers have observed a number of instances, however, where well-isolated dairymen and breeders have largely, if not completely, eradicated the pest from their herds by systematic destruction of the grubs.

In attempting to control the insect on the individual farm it is important to destroy the grubs in the young stock, and also to kill those larvæ which reach the backs rather late in the season.

POSSIBILITIES OF ERADICATION BY SYSTEMATIC DESTRUCTION OF GRUBS

For many years the possibilities of completely eliminating this destructive pest from given areas have been presented. In 1896 Osborn (73), after discussing methods of destroying the grubs, says:

While it is certain that this insect could be practically exterminated in the United States in a single year, we realize fully the great difficulty in getting every person owning cattle to know or appreciate the need of using the necessary means . . . We can not close this sketch of remedies without presenting a plan which, though it may be styled fanciful or ideal, must if carried out result in the extermination of the pest and the saving, we believe, of not less and probably more than \$50,000,000 per year to the farmers of the United States.

He then briefly outlines his plan of having all cattle examined and the grubs extracted or destroyed by chemical treatment. Other authors have presented somewhat similar suggestions, but until recently it would appear that the knowledge of the seasonal history of the two species of grubs in this country has been too meager to make possible the formulation of very definite plans. From studies which have been made in various parts of the world on this problem it appears certain that eradication from considerable areas, if not from entire countries, can be accomplished and that such effort would be very remunerative to the dairy and livestock industries. In considering the possibilities for eradication the following facts should be borne in mind:

1. Both species of *Hypoderma* confine their attack almost exclusively to domestic cattle. It is probable, however, that in vicinities where bison range these grubs might readily be carried over in numbers in such herds. Horses and goats are the only other hosts which would have to be considered at all, and the writers' observations clearly indicate that they would not play a part in perpetuating this species if all grubs were destroyed in bovines.

2. Every individual of both species of *Hypoderma* is present in the subcutaneous tissues of the backs of the cattle for a period in excess of 35 days, and while in this situation it is constantly amenable to treatments applied to the backs of the cattle or to extraction.

3. The larvæ are present in the subcutaneous tissues of the back during a fairly well-defined and comparatively limited period of the year.

The difficulty of carrying out systematic extraction or the application of ointments or washes under range conditions is at once apparent. In the farming and dairying sections, however, where the cattle are fairly gentle, systematic treatment would be fully warranted even under present conditions.

No definite experiments have been possible to show the distance the flies may travel, but circumstantial evidence indicates that they do not go far from the place where they hatch out, and this lends further encouragement to the efforts toward control. The writers' experience with the systematic destruction of grubs among animals on a single farm surrounded by infested cattle clearly indicates the futility of the individual attempting to secure a high degree of control, to say nothing of eradication. Cooperative community action is therefore clearly called for. Such an undertaking in Denmark is reported by Boas (5). On a farm in the center of an area where systematic grub extraction was carried out by a dairy association, the following numbers of grubs were found present and destroyed on seven succeeding years, beginning in 1889: 832, 215, 65, 229, 64, 0, 0. Complete eradication was not accomplished toward the edges of the areas covered by this effort, but the grubs were greatly reduced in numbers.

The stock raiser who has comparatively few grubs in his cattle has not been given sufficient consideration in connection with the sale of his cattle or hides, owing to the fact that it is the custom of the hide buyers of a section known to be infested by grubs to make a horizontal discount for grubbiness without determining the degree of infestation of the hides and even without the knowledge of the producer. With the inauguration of systematic control work there seems to be little doubt that hide buyers would pay a premium for hides from areas practicing control work, and also that butchers would slightly favor cattle from those areas.

In the initial undertaking of systematic control or eradication work it would seem desirable that the plan be attempted on a considerable area. Such a plan has been under consideration by the writers for several years, although funds have not been forthcoming to put it into effect (70). The writers believe that a large amount of educational work must be done in advance of any actual control work, and in this connection all organizations of business men and farmers should be thoroughly in sympathy with the undertaking. In an initial attempt it is thought best to have all of the work of destroying the grubs carried out by men specially trained in the procedure, and not to depend upon the volunteer efforts of the stock owners. It is probable that such an undertaking would have to be carried on during about three years, as inevitably a few grubs would escape destruction even in the most carefully executed plan. It ap-

pears that the mortality of grubs under natural conditions is high, and there is the possibility that with only an occasional grub maturing the male and female flies would fail to emerge at the same time and mating would not be possible. In carrying out such a plan it is imperative that an exact knowledge of the seasonal development of the grubs be obtained in advance, so that the date for beginning the work will be known with a fair degree of accuracy. Where both species of *Hypoderma* occur at least four treatments will be required. The first should be completed some days before the time of maturity of the earliest larvæ. All cattle exposed to fly attack should be carefully examined. In the greater part of the United States calves under 6 months old would not be found infested, but under certain conditions animals as young as 5 months of age may be infested.

The experiment carried out by Carpenter and his associates (18) on Clare Island, County Mayo, Ireland, amply demonstrates the possibility of complete eradication of grubs, provided all cattle are systematically treated.

The fact that a few cases of temporary sickness have resulted in cattle from careless hand extraction should not be allowed in any way to interfere with the work of destroying grubs in the backs of cattle. These cases are comparatively rare and the good accomplished by grub destruction far outweighs any loss which might be sustained.

LEGISLATION ON GRUB CONTROL

A very active interest is being shown in various parts of the world in the matter of grub control. Great Britain has for many years given attention to this problem, but her efforts took on more systematic form recently when the English Ministry of Agriculture in collaboration with the Scottish Board and the Department of Agriculture for Ireland formed a commission of experts to devise methods of control or eradication of the pest. It seems that there is a very strong sentiment in Great Britain in favor of the passage of laws to bring about the systematic destruction of the grubs. In Switzerland and France similar commissions have been organized recently; Germany (67) has had its commission functioning for several years; and in Denmark (26) a law was passed in 1923 by Parliament, looking toward the destruction of all grubs in cattle during the years 1923 and 1924 with a view to complete eradication throughout the nation.

This action by the legislative authorities of Denmark, it should be remembered, followed years of individual or community effort against the pest.

It is doubtful if any legislation on the part of our own country is advisable at present. After there have been large-scale demonstrations of what may be accomplished in the direction of grub eradication through well-organized cooperative work, however, appropriate legislative enactments will no doubt be called for.

SUMMARY

Cattle grubs of the genus *Hypoderma* are abundant throughout the greater part of the United States and southern Canada, and in

Germany, Switzerland, Denmark, Holland, and the British Isles, and probably occur throughout the remainder of Europe. They have been reported also from North Africa, western India, Mongolia, and parts of Japan. Of the two species, *H. bovis* De Geer is essentially a northern form as shown by its distribution, both in the United States and in Europe. In the United States *H. lineatum* is much more widely distributed than *H. bovis*, has been known for many more years, and has been bred from the native bison; possibly, therefore, it may be an American species, although now occurring in other parts of the world. *H. bovis*, on the other hand, appears to have been introduced into the United States from Europe rather recently.

Injury to cattle by these insects comes from (1) the annoyance caused by the flies during egg deposition and (2) the irritation produced by the larvæ within the bodies of the hosts. The yearly loss to the hide, tanning, and leather industries of the United States caused by these grubs is estimated at \$5,000,000 and the yearly losses to the people of the United States at \$50,000,000.

Cattle are the normal hosts for both *H. bovis* and *H. lineatum*. The American bison is also a host of *H. lineatum*. Although horses are attacked, in nature very few larvæ ever reach maturity in them. Goats may occasionally serve as hosts but in experiments with them, as also with sheep, dogs, rabbits, and guinea pigs, no larvæ were successfully reared. Several cases are known of the infestation of man by these parasites.

In several series of experiments with cattle controlled by muzzles and cages it was determined that the larvæ upon hatching from the eggs penetrate through the skin at the points where the eggs are laid and do not enter the host by the mouth, either in the egg or larval stage.

It was found that the place where the eggs are laid on the host has no apparent effect either on the place where the larvæ reach the subdermal tissues or on the time of their appearance. Larvæ entering the skin of an animal on the legs may go to the submucous layers of the gullet, as may also larvæ removed from the gullets and introduced by incision under the skin on the leg of a bovine.

H. lineatum prefers the heels as points for the attachment of its eggs, but eggs may be found on many other parts of the host. *H. bovis* oviposits on the legs, but more eggs are laid on the thighs and about the rumps of the cattle than with *H. lineatum*.

H. lineatum attaches its eggs in rows on the hairs; *H. bovis* deposits its eggs singly.

The usual incubation period for *H. lineatum* is from 3 to 6 days; for *H. bovis*, about 3 days.

After penetrating the skin the larvæ apparently work upward in the connective tissue and begin to appear in the chest and abdominal cavity about two months after penetration. Although many larvæ enter the connective tissue of the gullet it appears that many may never enter that organ. This is particularly true of *H. bovis*, as only one larva of this species was found among 1,140 specimens removed from 563 gullets in regions where this species abounds. Of 3,522 larvæ removed from 1,137 gullets, the majority were in the second stage, only a few being in the third.

The distance from the gullet and viscera to the subcutaneous tissues of the back is apparently traversed very rapidly by the larvæ. Soon after the larvæ reach the back they cut a hole through the skin. The duration of the third stage of *H. lineatum* after the skin of the back is punctured averaged 4.5 days at Dallas, Tex., and 4.26 days in New York; in *H. bovis* it averaged 3.35 days in New York. The average duration of the fourth stage of *H. lineatum* was 24.5 days and of *H. bovis*, 27.1 days. The development of the fifth stage of *H. lineatum* required an average of 30.3 days in Dallas, Tex., and that of *H. bovis* about 40 days in New York.

The total developmental period in the backs of cattle has been determined with fair accuracy in many individuals at points in Texas and New York. The three shortest developmental periods recorded at Dallas, Tex., were between 35 and 47, between 38 and 40, and between 39 and 46 days, respectively. The average at Dallas, Tex., was 56.3 days in one series and 57.7 days in another, whereas at Uvalde, Tex., it was 49.4 days. The developmental period of *H. bovis* in the backs of cattle in New York was 77 days (maximum), 65 days (minimum), and 72.8 days (average).

Mature larvæ may emerge from the host at any time of day or night, but the largest number as recorded by the writers emerged during the middle of the forenoon. The time from emergence from the host to appearance of the flies of *H. lineatum* at Dallas, Tex., ranged from 18 to 77 days, with an average of 41.7 days. In the case of *H. bovis* at Middletown, N. Y., this period ranged from 22 to 45 days, with an average of 31.34 days.

Mating of the adults of *H. lineatum* takes place very soon after emergence, and oviposition may begin a few minutes after copulation. There are some distinct differences in the habits of oviposition of *H. lineatum* and *H. bovis*. Among other things the flies of the latter species are more persistent in their attack on the cattle and induce greater fear in them. *H. lineatum* may oviposit at a temperature as low as between 40 and 45° F., but oviposits freely between 55 and 85° F.

The adults of *H. lineatum* lived in captivity from 1 to 25 days. The average life of the adults of this species is about 5 or 6 days and *H. bovis* has a similarly brief life span.

The seasonal history of *H. lineatum* varies widely according to latitude and other conditions. In southwestern Texas the flies may appear and lay eggs in the fall or early winter so that the whole life cycle may be correspondingly earlier than elsewhere in the country. As the higher latitudes and altitudes are approached the various stages in the life history are later. In the northern edge of the United States the adults do not begin to emerge until about April 1. The seasonal development of the larvæ is closely correlated with that of oviposition; for instance, in southwestern Texas the earliest grubs may reach the backs of the cattle in July, at Dallas, Tex., in September or October, at Ames, Iowa, during January, and at Herkimer, N. Y., in February. The earliest appearance of the larvæ of *H. bovis* in the backs of cattle is somewhat later than that of *H. lineatum*. The dates in different regions when the earliest larvæ become mature and leave the host, and the dates when the last larva has reached the back, are matters of much importance in connection with control

and have been determined and mapped with a fair degree of accuracy in several parts of the country. In general the duration of infestation of the backs of cattle with *H. bovis* is longer than with *H. lineatum*, owing to the longer developmental period required by *H. bovis*.

Temperature, humidity, cloudiness, and drainage are important factors in natural control. Host resistance as acquired by age is also an important factor in holding down the abundance of *Hypoderma*. No important insect enemies or diseases affecting *Hypoderma* have been found.

The most effective time for the practice of control procedure is during the period of development of the larvæ in the subcutaneous tissues of the back. Destruction of the larvæ may be accomplished by hand extraction with or without the aid of forceps. In the case of certain breeds of cattle extraction of the grubs is very difficult.

Tests of the application of washes, powders, and ointments to the backs of the cattle and also the injection of substances into the cysts containing the larvæ show that each of these methods of treatment is effective if certain materials are used. Among the most effective should be mentioned: Derris used as a wash, as an ointment, or as a powder; iodoform used as an ointment; pyrethrum applied as an ointment; benzol and carbon tetrachloride injected into the grub cysts; fine tobacco applied in powder form and nicotine dust applied dry.

No adverse effects on the host have been observed in this country from the destruction of the grubs in the backs of cattle with suitable insecticides.

The cost of extraction or treatment depends on the skill of the operator but in all cases it is small compared with the benefits derived.

Experiments with the application to the feet and legs of cattle of certain insecticides and repellents by means of wading vats show that with the materials used control was not brought about, and indicate that attack directed against the eggs or young larvæ in this way will not be successful.

Results of individual effort against cattle grubs is likely to be disappointing, especially if the work is not thoroughly done and if untreated cattle are in close proximity to the treated herd.

Systematic treatment of all infested cattle in a neighborhood either by extraction or by the use of insecticides appears to be a practical method of control or eradication. Although these methods are best adapted to dairy or farm conditions it is probable that they may be modified so as to be applied successfully to range cattle.

In order successfully to combat the insects by destroying the larvæ in backs of cattle it is necessary to treat all infested cattle at intervals of not to exceed 35 days. The first treatment must be given before the earliest larvæ have matured and left the host. In most parts of the United States it is necessary to treat the animals four times during a season to reach all of the larvæ. The time of beginning the treatments in different parts of the country is indicated in the discussion of seasonal history.

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